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FISHERY BULLETIN, VOLUME 73, NUMBER 4, OCTOBER 1975

Bruce B. Collette, et al

National Marine Fisheries Service
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October 1975

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7. AUTHOR(S)
Dr. Bruce B. Collette (Editor)

8. REPORT NO.

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15. PUBLICATION REFERENCE
Fishery Bulletin - Vol. 73, No. 4, October 1975
National Marine Fisheries Service

16. ABSTRACT

The Fishery Bulletin is issued quarterly by the National Marine Fisheries Service and carries original research reports and technical notes on investigations in fishery science, engineering, and economics. This issue contains articles concerning: Marine trophic interactions, Coho salmon, Mesopelagic micronekton, Penaeid shrimp, American Samoa longline fishery, Golden shiner, Zooplankton relationships, Chinook salmon and steelhead trout, the genus Nematoscelis, Microcarnivorous fishes, Fishery regulation, Atlantic sturgeon, Pink and chum salmon, American lobster, Fish populations, Zebrafish, Cunner and young tautog, Dungeness crabs, Mesopelagic fishes, Alaska plaice, Rock sole, Yellowfin sole, Pacific salmon, and Gas bubble disease. (ETJA)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fisheries, *Fishes, *Periodicals, *Marine fishes, Aquaculture, Aquatic animals, Seafood, Shellfish, Aquatic biology, Marine biology, Invertebrates, Vertebrates, Fresh water fishes, Fishing, Fishing grounds, Salmon, Shrimp, Trout, Lobster, Crabs, Zooplankton

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Fishery science, *Fishery periodicals, *Fishery reports, *Fishery research, Fishing economics, Marine trophic relationships, Mesopelagic micronekton, Nematoscelis, Sturgeon, Zebrafish, Sole fish, Fish diseases

17C. COSATI FIELD/GROUP

6C, 8A, 6H, 6E

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1. NOAA ACCESSION NUMBER
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4. TITLE AND SUBTITLE
Marine Trophic Interactions by Dynamic Simulation of Fish Species

5. REPORT DATE

6.

7. AUTHOR(S)
James D. Parrish

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Massachusetts Cooperative Fishery Unit,
U.S. Fish and Wildlife Service,
University of Massachusetts,
Amherst, MA 01002

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15. PUBLICATION REFERENCE
Marine Trophic Interactions by Dynamic Simulation of Fish Species - from Fishery Bulletin, Vol. 73, No. 4, 1975

16. ABSTRACT

A mathematical model was developed for performing dynamic simulations of interacting animal species. The energy balance of the individual animal was modeled so that growth and reproduction respond to food consumption after metabolic expenses are met. Population change in response to recruitment (based on parental spawning) and mortality from natural causes, predation, starvation, and (where applicable) human exploitation. The forms of the various component mathematical functions were derived from the available ecological sources. Functions and parameters are especially applicable to marine fish species. Trophic webs of any size or form can be constructed using this basic species model. Computer solution of the essentially continuous differential model gives a time history of trophic and population variables for all species in the web. Models of trophic webs of 2, 3, and 4 levels were constructed and exercised. These were used to examine effects of age class structure, reproductive time lag, and population regulation by starvation mortality and fecundity control. Competition between species and the effects of a top predator on competitors, with and without human exploitation, were studied. (Author modified)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Marine fishes, *Animal behavior, *Animal ecology, *Food chains, Food consumption, Seafood, Feeding habits, Primary biological productivity, Mathematical models, Aquatic animals, Aquaculture

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Marine trophic interactions, *Dynamic simulation, *Fish species, *Trophic ecology, *Tropic web, *Fish models, Animal competition, Animal reproduction, Trophic analysis, Fish dynamics, Fish populations

17C. COSATI FIELD/GROUP

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1. NOAA ACCESSION NUMBER
NOAA-75122301-2

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3. RECIPIENT'S ACCESSION NUMBER
PB248 861-04-2

4. TITLE AND SUBTITLE
Homing Behavior and Contribution to Columbia River Fisheries of Marked Coho Salmon Released at Two Locations

5. REPORT DATE

6.

7. AUTHOR(S)
Robert R. Vreeland, Roy J. Wahle, and Arthur H. Arp

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Columbia Fisheries Program Office, & Division of River Basin
National Marine Fisheries Service, Studies, U.S. Fish and
NOAA, Wildlife Service,
Portland, OR 97208 Portland, OR 97232

10. PROJECT/TASK NO.

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12. SPONSORING ORGANIZATION NAME AND ADDRESS
National Marine Fisheries Service, NOAA
Washington, DC 20235

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15. PUBLICATION REFERENCE
Homing Behavior and Contribution to Columbia River Fisheries of Marked Coho Salmon Released at Two Locations - from Fishery Bulletin: Vol. 73, No. 4, 1975

16. ABSTRACT This study was initiated to determine the feasibility of creating or enhancing fisheries in specific areas by releasing salmon smolts into those areas. In 1970 two groups each of approximately 100,000 1968-brood coho salmon, Oncorhynchus kisutch, were marked with a right ventral (RV) or a left ventral (LV) finclip at Little White Salmon National Fish Hatchery, near Cooks, Wash. The LV-marked group were released at Youngs Bay and the RV-marked group were released at Little White Salmon Hatchery. The Youngs Bay and Columbia River gill-net fisheries were sampled for these marks in the fall of 1970 and 1971. The two groups homed to their respective areas of release with very little straying. The LV-marked group contributed 7.7 fish to the fisheries sampled for each 1,000 fish released, and the RV-marked group contributed 11.7 fish to the fisheries sampled per 1,000 fish released. However, a fair comparison of the contribution of the two groups is inhibited by 1) incomplete sampling for these marks in the ocean fisheries, 2) the difference in time and size of release of the groups, 3) the unknown effect of delayed mortality due to hauling the LV-marked group, and 4) duplication of these marks in the ocean fisheries. (Author modified)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Fisheries, *Salmon, *Fresh water fishes, *Sampling, Aquatic animals, Marine fishes, Fishing grounds, Aquaculture, Vertebrates, Oceans, Marking, Animal behavior, Animal migrations

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Homing behavior, *Columbia River fisheries, *Marked salmon, *Coho salmon, *Salmon smolts, *Salmon migrations, Fish hatchery, Ocean fisheries, Pacific salmon, Salmon experiments, Salmon tests, Commercial salmon fisheries

17C. COSATI FIELD/GROUP

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1. NOAA ACCESSION NUMBER
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3. RECIPIENT'S ACCESSION NUMBER
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4. TITLE AND SUBTITLE
Mesopelagic Micronekton in Hawaiian Waters: Faunal Composition, Standing Stock, and Diel Vertical Migration

5. REPORT DATE

6.

7. AUTHOR(S)
Sherwood D. Maynard, Fletcher V. Riggs, & John F. Walters

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Department of Oceanography,
University of Hawaii,
Honolulu, HI 96822

10. PROJECT/TASK NO.

11. CONTRACT/GRANT NO.
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12. SPONSORING ORGANIZATION NAME AND ADDRESS
National Science Foundation &
University of Hawaii, Department of Oceanography &
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15. PUBLICATION REFERENCE
Mesopelagic Micronekton in Hawaiian Waters: Faunal Composition, Standing Stock, and Diel Vertical Migration; from Fishery Bulletin, Vol. 73, No. 4, 1975; Grant GA-33659

16. ABSTRACT
On one cruise off leeward Oahu, Hawaii, micronekton from 9 deep-oblique mid-water trawl tows (0-1,200 m) and a 24-h series of 14 consecutive shallow-oblique tows (0-400 m) were sorted into 16 faunal groups, enumerated, and weighed. Diel-related trawl avoidance was not significant in deep tows. Mean total micronekton standing stocks for the deep tows were 898 organisms/100 m^2 ocean surface and 494 g (wet weight)/100 m^2 ocean surface. Fishes comprised half of the total numbers and biomass, while crustaceans contributed one-third of the total numbers and one-fifth of the biomass. Of the micronekton deeper than 400 m during the day, 43% of the number of organisms with 47% of the biomass migrated into the upper 400 m at night. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Nekton, *Biomass, *Aquatic animals, Sampling, Zooplankton, Animal behavior, Cephalopoda, Invertebrates, Mollusca, Crustacea, Shellfish, Seafood, Aquaculture, Animal migrations, Fishing, Salinity

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Micronekton, *Mesopelagic micronekton, *Hawaiian waters, *Faunal composition, *Diel vertical migration, *Fishery Bulletin, Fish trawling, Oceanic ecosystem, Micronekton sampling, Micronekton populations, Faunal groups

17C. COSATI FIELD/GROUP

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18. AVAILABILITY STATEMENT
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1. NOAA ACCESSION NUMBER NOAA-75122301-4	2.	3. RECIPIENT'S ACCESSION NUMBER PB248 861-04-4

4. TITLE AND SUBTITLE Description and Biology of a New Species of Pelagic Penaeid Shrimp, Bentheogennema Burkenroadi, From the Northeastern Pacific	5. REPORT DATE
	6.
7. AUTHOR(S) Earl E. Krygier and Robert A. Wasmer	8. REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS School of Oceanography, Oregon State University, Corvallis, OR 97331	10. PROJECT/TASK NO.
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12. SPONSORING ORGANIZATION NAME AND ADDRESS Office of Naval Research & Atomic Energy Commission	13. TYPE OF REPORT AND PERIOD COVERED
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15. PUBLICATION REFERENCE

Description and Biology of a New Species of Pelagic Penaeid Shrimp, Bentheogennema Burkenroadi, From the Northeastern Pacific - from Fishery Bulletin, Vol. 73, No. 4,'75

16. ABSTRACT

The new species of pelagic penaeid shrimp lacks the richly plumose arthrobranch described for the genus and has a single pair of terminal spines on the telson. It is found mainly in transitional water of the North Pacific between 500 and 1,000 m by day and 150 and 1,000 m at night. Examination of testes and ovaries, and the structures of the petasma and thelycum, indicates a 4-5 mo spawning season and an equal male to female sex ratio. Generation time was estimated to be 2 yr. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Shrimps, *Crustacea, *Shellfish, *Arthropoda, *Aquatic biology, *Marine biology, Sampling, Aquaculture, Fishes, Fishing grounds, Taxonomy, Reproduction (biology)

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Pelagic penaeid shrimp, *Penaeid shrimp, *Bentheogennema Burkenroadi, *North Pacific waters, Shrimp biology, Shrimp systematics, Shrimp taxonomy, Shrimp spawning, Shrimp reproduction, Shrimp growth, Spawning

17C. COSATI FIELD/GROUP

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1. NOAA ACCESSION NUMBER: NOAA-75122301-5

2.

3. RECIPIENT'S ACCESSION NUMBER: PB248 861-04-5

4. TITLE AND SUBTITLE: The American Samoa Longline Fishery, 1966-71

5. REPORT DATE

6.

7. AUTHOR(S): Howard O. Yoshida

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS

Southwest Fisheries Center Honolulu Laboratory,
National Marine Fisheries Service, NOAA
Honolulu, HI 96812

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12. SPONSORING ORGANIZATION NAME AND ADDRESS

National Marine Fisheries Service, NOAA
Washington, DC 20402

13. TYPE OF REPORT AND PERIOD COVERED

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15. PUBLICATION REFERENCE

The American Samoa Longline Fishery, 1966-71 - from Fishery Bulletin, Vol. 73, No. 4, 1975

16. ABSTRACT

Aspects of the longline fishery based at American Samoa covering the period from 1966 to 1971 are described. The fishery is discussed primarily as it relates to the albacore, Thunnus alalunga, and to a small extent the yellowfin tuna, T. albacares. The landings of albacore fluctuated between 17,722 and 28,310 metric tons from 1966 to 1971. Although no downward trend was evident in the relation between total landings and total effort, the relation between CPUE (catch per unit of effort) and effort showed a definite downward trend. Generally fishing effort was confined to the north of lat. 20°S in the first and fourth quarters. In the second and third quarters large amounts of effort were also expended south of lat. 20°S. The length-frequency distribution of albacore showed that albacore sizes were stratified by latitude. North of lat. 20°S the size of albacore was rather uniform, in that only a single mode was evident in the length-frequency distributions. South of lat. 20°S two or more modes were evident. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishing, *Fishes, *Fishing grounds, *Tunas, *Fisheries, *Marine fishes, Vertebrates, Aquatic animals, Aquaculture, Seafood, Canneries, Oceans, Surface waters, Sampling

17B. IDENTIFIERS/OPEN-ENDED TERMS

*American Samoa longline fishery, *Longline fisheries, *Albacore, *Yellowfin tuna, *Albacore landings, *Tuna landings, *Fishery bulletin, Thunnus alalunga, Thunnus albacares, Fishery resources, Tuna canneries, Tuna fishing, Tuna distributions, Albacore size, Tuna growth

17C. COSATI FIELD/GROUP

6C, 8A

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1. NOAA ACCESSION NUMBER NOAA-75122301-6	2.	3. RECIPIENT'S ACCESSION NUMBER PB248 861-04-6

4. TITLE AND SUBTITLE
Effects of Photoperiod-Temperature Regimes and Pinealectomy on Body Fat Reserves in the Golden Shiner, Notemigonus Crysoleucas

5. REPORT DATE

6.

7. AUTHOR(S)
Victor L. De Vlaming

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Biology Department,
Marquette University,
Milwaukee, WI 53233

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12. SPONSORING ORGANIZATION NAME AND ADDRESS
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13. TYPE OF REPORT AND PERIOD COVERED

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15. PUBLICATION REFERENCE
Effects of Photoperiod-Temperature Regimes and Pinealectomy on Body Fat Reserves in the Golden Shiner, Notemigonus Crysoleucas - from Fishery Bulletin, V. 73, No. 4, '75

16. ABSTRACT Various photoperiod-temperature regimes were examined for their effects on total fat content (excluding gonads) in Notemigonus crysoleucas; experiments were conducted during several different phases of the reproductive cycle. In Notemigonus, fattening normally occurs in fall and early winter concomitant with the early phases of gonadal development. Body fat stores are progressively depleted during the prespawning and spawning seasons. Results showed that the effects of photoperiod-temperature regimes on lipid metabolism are apparently not totally dependent on the effects of these environmental factors on reproduction. The effects of pinealectomy on lipid reserves varied depending on the phase of the natural reproductive cycle when the organ was removed, as well as, with the photoperiod-temperature regime under which the experimental animals were maintained. It was shown that pinealectomy reverses the effects of photoperiod on lipid metabolism at a particular temperature. Results suggest that the pineal body is involved in regulating physiological functions and may serve as a photoreceptor and/or transducer of photoperiod information.
(Author modified)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Shiners, *Fresh water fishes, *Photoperiods, *Fat analysis, Lipids, Fishes, Marine fishes, Vertebrates, Body fat, Lipid metabolism, Reproduction (biology)

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Golden shiner, *Notemigonus Crysoleucas, *Pinealectomy, *Photoperiod-temperature regimes, *Body fat reserves, *Lipid reserves, Gonadal development, Telost fishes, Fat metabolism

17C. COSATI FIELD/GROUP

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1. NOAA ACCESSION NUMBER
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3. RECIPIENT'S ACCESSION NUMBER
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4. TITLE AND SUBTITLE
Relationships Between Zooplankton Displacement Volume, Wet Weight, Dry Weight, and Carbon

5. REPORT DATE

6.

7. AUTHOR(S)
Peter H. Wiebe, Steven Boyd, and James L. Cox

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Woods Hole Oceanographic Institution, & Southeastern Massachusetts University
Woods Hole, MA 02747
North Dartmouth, MA 02747

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11. CONTRACT/GRANT NO.
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National Science Foundation &
National Marine Fisheries Service, NOAA
Washington, DC 20235

13. TYPE OF REPORT AND PERIOD COVERED

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15. PUBLICATION REFERENCE
Relationships Between Zooplankton Displacement Volume, Wet Weight, Dry Weight, and Carbon - Contribution No. 3433; from Fishery Bulletin, Vol. 73, No. 4, 1975

16. ABSTRACT Interconversion of various measures of zooplankton biomass have great utility in studies requiring nondestructive techniques, or for interpretation of past data. In establishing predictive relationships between such measures, the appropriate regression to use is the geometric mean estimate, which provides a regression line in which the regressions of X on Y and Y on X are identical. This type of analysis was employed in determinations on samples from diverse sea areas in different seasons and it was determined that statistically significant relationships exist between carbon, wet weight, displacement volume, and dry weight when a constant technique is used. Comparability of different techniques for a biomass measurement may be poor, especially in the case of displacement volume and wet weight measurements due to variations in the interstitial water content. Moreover, interstitial water content varies inversely with total biomass density, which accounts for the absence of a simple percentage relationship between wet weight or displacement volume and other measures of zooplankton biomass. (Author modified)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Zooplankton, *Biomass, *Weight (mass), *Weight measurement, *Carbon, Plankton, Aquatic animals, Aquatic plants, Aquatic biology, Oceans, Displacement, Sampling

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Zooplankton biomass, *Wet weight, *Dry weight, *Displacement volume, *Biomass measures, *Biomass samples, Caloric values, Zooplankton collection, Regression equations

17C. COSATI FIELD/GROUP

6C, 8A

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1. NOAA ACCESSION NUMBER NOAA-75122301-8	2.	3. RECIPIENT'S ACCESSION NUMBER PB248 861-04-8

4. TITLE AND SUBTITLE Effects of Various Concentrations of Dissolved Atmospheric Gas on Juvenile Chinook Salmon and Steelhead Trout	5. REPORT DATE 6.
7. AUTHOR(S) Earl M. Dawley and Wesley J. Ebel	8. REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS Northwest Fisheries Center, National Marine Fisheries Service, NOAA Seattle, WA 98112	10. PROJECT/TASK NO. 11. CONTRACT/GRANT NO.
12. SPONSORING ORGANIZATION NAME AND ADDRESS National Marine Fisheries Service, NOAA Washington, DC 20235	13. TYPE OF REPORT AND PERIOD COVERED 14.

15. PUBLICATION REFERENCE

Effects of Various Concentrations of Dissolved Atmospheric Gas on Juvenile Chinook Salmon and Steelhead Trout - from Fishery Bulletin, Vol. 73, No. 4, 1975

16. ABSTRACT Bioassays in shallow tanks (25 cm deep) with dissolved nitrogen and argon gas concentrations ranging from 100 to 125% of saturation in water at 15°C were conducted to determine lethal and sublethal effects on juvenile chinook salmon, *Oncorhynchus tshawytscha*, and steelhead trout, *Salmo gairdneri*. Significant mortality of both species commenced at 115% saturation of nitrogen and argon (111% saturation of total dissolved atmospheric gas pressure). Over 50% mortality of both steelhead and chinook occurred in less than 1.5 days in water at 120 and 125% of saturation. Significant differences in swimming performance, growth, and blood chemistry were measured in groups of fish tested at sublethal exposures in various concentrations of dissolved gases. Sublethal stress for 35 days at 110% dissolved nitrogen (106% total atmospheric gas) decreased normal swimming ability of chinook. Growth of both steelhead and chinook was affected by sublethal exposures in water saturated with atmospheric nitrogen and argon at 105, 110, and 115%. Blood chemistry was affected at sublethal exposures in water at 115% saturation. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Salmon, *Trout, *Fresh water fishes, *Marine fishes, Aquatic animals, Vertebrates, Fishes, Bioassay, Rare gases, Argon, Nitrogen, Gases, Surface waters, Rivers, Animal diseases, Sampling

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Dissolved atmospheric gases, *Atmospheric gases, *Chinook salmon, *Steelhead trout, *Argon gas, *Nitrogen gas, *Pacific salmon, *Oncorhynchus tshawytscha*, *Salmo gairdneri*, Gas saturation, Gas bubble disease, Fish mortality

17C. COSATI FIELD/GROUP

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1. NOAA ACCESSION NUMBER
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3. RECIPIENT'S ACCESSION NUMBER
PB248 861-04-9

4. TITLE AND SUBTITLE
Biology and Taxonomy of the Genus *Nematoscelis* (Crustacea, Euphausiacea)

5. REPORT DATE

6.

7. AUTHOR(S)
K. Gopalakrishnan

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Scripps Institution of Oceanography,
La Jolla, CA 92037

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15. PUBLICATION REFERENCE
Biology and Taxonomy of the Genus *Nematoscelis* (Crustacea, Euphausiacea) - from *Fishery Bulletin, Vol. 73, No. 4, 1975 - Grant GA 31783*

16. ABSTRACT
The seven species of *Nematoscelis*, *N. difficilis*, *N. megalops*, *N. gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, and *N. lobata*, are described in a comparative manner, and keys for their identifications are provided. The key to the larvae is based on structural differences in the carapace and rostrum of furcilia stages, whereas the key to adults is mostly based on diagnostic features of the first thoracic leg (maxilliped) and a male secondary sexual structure, the petasma. *Nematoscelis gracilis* is represented by two distinct forms; they are considered ecophenotypes, since their patterns of geographical distribution appear correlated with differences in environmental characteristics, particularly the distribution of dissolved oxygen in the water column. Diagnostic features of these forms are pointed out. The antennule and carapace are sexually dimorphic in adults of all *Nematoscelis*. Abdominal photophores in the males show species-specific patterns of enlargement. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Crustacea, *Taxonomy, *Marine biology, *Shellfish, *Arthropoda, Aquatic animals, Invertebrates, Larvae, Aquatic biology, Aquaculture, Reproductive system, Musculoskeletal system, Seafood, Fishes

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, **Nematoscelis*, *Euphausiacea, *Crustacea differences, **N. difficilis*, *N. megalops*, *N. gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, *N. lobata*, Larval differences, Petasma, Phylogenetic associations

17C. COSATI FIELD/GROUP

6C, 8A, 6P

18. AVAILABILITY STATEMENT
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4. TITLE AND SUBTITLE
Food, Activity, and Habitat of Three "Picker-Type" Microcarnivorous Fishes in the Kelp Forests off Santa Barbara, California

5. REPORT DATE

6.

7. AUTHOR(S)
Richard N. Bray and Alfred W. Ebeling

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Marine Sciences Institute and Department of Biological Sciences
University of California,
Santa Barbara, CA 93106

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15. PUBLICATION REFERENCE
Food, Activity, and Habitat of Three "Picker-Type" Microcarnivorous Fishes in the Kelp Forests off Santa Barbara,California - from Fishery Bulletin, V. 73, No. 4, 1975

16. ABSTRACT

Diets, daily activity, and habitat preference were compared between the kelp perch, Brachyistius frenatus; the señorita, Oxyjulis californica; and the white seaperch, Phanerodon furcatus, all of which co-occur in areas of reef and kelp off Santa Barbara, Calif. The kelp perch and señorita often clean ectoparasites off larger host fishes, whereas the white seaperch is a more generalized picker-type microcarnivore. The kelp perch and señorita, which co-occur in the kelp canopy, showed the least amount of total overlap in resource use, expressed as a combination of individual overlaps in food, activity, and habitat. The señorita had the narrowest breadth of diet but the widest breadth of habitat (within the kelp-bed areas). Señoritas and white seaperch ate mostly bryozoans encrusted on plants, whereas kelp perch ate mostly plankton and other tiny motile prey. As species, neither the kelp perch nor the señorita derives substantial amounts of food from cleaning, although some individual señoritas may. Unlike the two "cleaners," the white seaperch also ate substantial numbers of bottom prey. None of the species forage at night.
(Author modified)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Perch, *Marine fishes, *Fresh water fishes, Carnivora, Aquatic animals, Fishing, Fishing grounds, Taxonomy, Vertebrates, Aquaculture, Sampling, Food habits, Animal behavior

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Microcarnivorous fishes, *Kelp perch, *Señorita, *White seaperch *Picker-type microcarnivore, Fish habitats, Fish activity, Fish food habits, Fish behavior, Sea Grant Program

17C. COSATI FIELD/GROUP

6C, 8A

18. AVAILABILITY STATEMENT Freeman	19. SECURITY CLASS (This report) UNCLASSIFIED	21. NO. OF PAGES 16
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1. NOAA ACCESSION NUMBER
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4. TITLE AND SUBTITLE
Fishery Regulation Via Optimal Control Theory

5. REPORT DATE

6.

7. AUTHOR(S)
William J. Palm

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
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12. SPONSORING ORGANIZATION NAME AND ADDRESS
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15. PUBLICATION REFERENCE
Fishery Regulation Via Optimal Control Theory - from Fishery Bulletin, Vol. 73, No. 4, 1975 - Sea Grant #98-20-6807C

16. ABSTRACT

This paper attempts to show how control theory can be used to formulate a regulatory scheme for fisheries. The regulatory mechanism considered is a limit imposed on fishing effort. It is shown that static optimization methods, such as maximum equilibrium yield analysis, need to be supplemented with dynamic methods, such as optimal control theory, which take into account the variable nature of a fishery. The dynamic analysis is used to show that the size of a limit on effort should be a feedback function of the variables in the state of the fishery. The concept of the Linear-Quadratic Optimal Control Problem is introduced as a method for devising such a feedback scheme for fishery regulation. A single-variable logistic model is used to introduce the basic concepts. A model with three variables is then analyzed to show how the techniques are easily extended to the general multivariable case. Details of the general method are given in an Appendix. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fisheries, *Control theory, *Fishing, *Regulations, *Equilibrium methods, *Dynamic structural analysis, Mathematical models, Management, Stochastic processes, Time series analysis, Computer programming

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Fishery regulation, *Optimal Control theory, *Regulatory mechanisms, *Fishing efforts, *Linear-Quadratic Optimal Control Problems, *Maximum equilibrium yield analysis, Bang-bang control approach, Fishery management

17C. COSATI FIELD/GROUP

12A, 6C, 5A, 5C

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1. NOAA ACCESSION NUMBER NOAA-75122301-12	2.	3. RECIPIENT'S ACCESSION NUMBER PB248 861-04-12

4. TITLE AND SUBTITLE
Differentiation of Freshwater Characteristics of Fatty Acids in Marine Specimens of the Atlantic Sturgeon, Acipenser Oxyrhynchus

5. REPORT DATE

6.

7. AUTHOR(S)
R.G. Ackman, C.A. Eaton, and B.A. Linke

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Environment Canada,
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Halifax, Nova Scotia B3J 2R3 Can.

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12. SPONSORING ORGANIZATION NAME AND ADDRESS
National Marine Fisheries Service, NOAA
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13. TYPE OF REPORT AND PERIOD COVERED

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15. PUBLICATION REFERENCE
Differentiation of Freshwater Characteristics of Fatty Acids in Marine Specimens of the Atlantic Sturgeon, Acipenser Oxyrhynchus from Fishery Bulletin, V. 73, No. 4 '75

16. ABSTRACT Lipids and fatty acids of two marine-caught specimens of the Atlantic Sturgeon, Acipenser oxyrhynchus, which spawns and also feeds in freshwater, were examined. Specific fat contents, respectively 47.2 and 25.0% in orange-colored dorsal tissue and 8.5% in both livers, were high but not unexpected for sturgeons generally. In each fish a very consistent basic fatty acid composition of depot fats showed that this fat in various parts of the body had a common function. Depot fat from the fatter fish had high iodine values (ca. 190) while in the leaner fish values were lower (ca. 135) and more typical of sturgeons generally. The fatty acid details of depot fats showed some characteristics of marine fats, such as the presence of the unusual $\omega1$ and $\omega4$ polyunsaturated fatty acids, the low figure for linoleic acid and relatively high proportions of long chain polyunsaturated fatty acids, but were more typical of freshwater fats in the virtual absence of eicosenoic and docosenoic acids. Broadly speaking, the fatty acids of the Atlantic sturgeon seem to place it in a special class of fish with fats generally resembling freshwater fish fats in composition, despite its marine origin. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Fatty acids, *Fats, *Fat analysis, *Lipids, *Fresh water fishes, Aquatic animals, Marine fishes, Sampling, Oils, Muscles, Gas chromatography, Invertebrates

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Atlantic sturgeon, *Acipenser oxyrhynchus, *Depot fats, *Fish fats, *Sturgeon fats, *Sturgeon lipids, *Fatty acid analysis, Marine specimens, Freshwater characteristics, Polar lipids, Triglycerides

17C. COSATI FIELD/GROUP

6C, 8A, 6A, 7C

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1. NOAA ACCESSION NUMBER NOAA-75122301-13	2.	3. RECIPIENT'S ACCESSION NUMBER PB248 861-04-13

4. TITLE AND SUBTITLE Zooplankton Abundance and Feeding Habits of Fry of Pink Salmon, Oncorhynchus Gorbuscha, and Chum Salmon, Oncorhynchus Keta, In Traitors Cove, Alaska, With Speculations On the Carrying Capacity of the Area

5. REPORT DATE

6.

7. AUTHOR(S)
Jack E. Bailey, Bruce L. Wing, and Chester R. Mattson

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Northwest Fisheries Center Auke Bay Laboratory,
National Marine Fisheries Service, NOAA
Auke Bay, AK 99821

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15. PUBLICATION REFERENCE Zooplankton Abundance and Feeding Habits of Fry of Pink Salmon, Oncorhynchus Gorbuscha, and Chum Salmon, Oncorhynchus Keta, In Traitors Cove, Alaska, With Speculations On the Carrying Capacity of the Area -Fishery Bulletin, V. 73, No.4

16. ABSTRACT

Juvenile pink salmon, Oncorhynchus gorbuscha, and chum salmon, O. keta, 28 to 56 mm long (fork length) from Traitors River in southeastern Alaska, fed little in freshwater but fed heavily in the estuary, mainly on pelagic zooplankters. Fry did not feed on cloudy moonless nights. The rate of evacuation of pink salmon stomachs ranged from 6 h at 12.8°C to 16 h at 8.5°C. The abundance of zooplankton ranged from 9 to 154 organisms per liter and quantitatively did not change noticeably while fry were in the estuary. In 1964, 1965, and 1966, the estimated numbers of fry in Traitors Cove was 7, 1, and 4 million, respectively. An attempt was made to estimate the carrying capacity of Traitors Cove, using food consumption and evacuation rates in conjunction with estimates of standing crop of zooplankton. It was concluded that 50 to 100 million additional fry from hatcheries would probably exceed the carrying capacity of the estuary. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Salmon, *Zooplankton, *Fresh water fishes, Estuaries, Food habits, Marine fishes, Fishes, Sampling, Aquatic animals, Aquaculture, Food consumption, Fishing grounds, Vertebrates

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Zooplankton abundance, *Feeding habits, *Pink salmon, *Salmon fry, *Chum salmon, *Traitors Cove, AK, *Oncorhynchus Gorbuscha, *Oncorhynchus Keta, *Fishery Bulletin, Pelagic zooplankters, Salmon feeding, Salmon hatcheries, Alaskan hatcheries

17C. COSATI FIELD/GROUP

6C, 8A

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1. NOAA ACCESSION NUMBER
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3. RECIPIENT'S ACCESSION NUMBER
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4. TITLE AND SUBTITLE
Effects of Trap Selectivity and Some Population Parameters on Size Composition of the American Lobster, Homaris Americanus, Catch Along the Maine Coast

5. REPORT DATE

6.

7. AUTHOR(S)
Jay S. Krouse and James C. Thomas

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Maine Department of Marine Resources,
West Boothbay Harbor, ME 04575

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12. SPONSORING ORGANIZATION NAME AND ADDRESS
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15. PUBLICATION REFERENCE
Effects of Trap Selectivity and Some Population Parameters on Size Composition of the American Lobster, Homaris Americanus, Catch Along the Maine Coast - Fishery Bulletin

16. ABSTRACT

Information collected aboard commercial lobster boats along the Maine coast (1971-73) revealed, among other things, high numbers of sublegal lobsters (<81 mm carapace length) being handled by fishermen while sorting their catches. Throw-back rations of illegal to legal lobsters (1.8 to 12.4:1) varied in association with lath spacing. Traps with spacings of 1 5/8 to 1 3/4 inches accounted for markedly fewer sublegals than those traps with 1 1/4- to 1 1/2-inch spacings. Selectivity curves calculated for research traps with escape ports of 1 1/2, 1 5/8, and 1 3/4 inches and a trap escapement study demonstrate that a spacing of 1 3/4 inches is large enough to allow escapement of most sublegals yet small enough to retain legal lobsters. A regression of carapace length on carapace width shows that only an insignificant percentage of legal lobsters could physically squeeze through a 1 3/4-inch opening. Thus, results of this study led us to recommend that with a minimum legal length of 81 mm, traps should have 1 3/4-inch escape vents. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Lobsters, *Shellfish, *Crustacea, *Arthropoda, *Fishing, Invertebrates, Aquatic animals, Fishing grounds, Fishes, Coasts, Sampling, Fisheries, Seafood

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *American lobster, *Homarus Americanus, *Trap selectivity, *Maine coastal waters, *Lobster fishing, *Lobster fishermen, *Lobster traps, Sublegal lobsters, Culls, Lobster fisheries, Fishing traps, Lath spacing

17C. COSATI FIELD/GROUP

6C, 8A

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1. NOAA ACCESSION NUMBER NOAA-75122301-15	2.	3. RECIPIENT'S ACCESSION NUMBER PB248 861-04-15

4. TITLE AND SUBTITLE Experimental Exploitation of Competing Fish Populations	5. REPORT DATE
	6.
7. AUTHOR(S) Ralph P. Silliman	8. REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS Northwest Fisheries Center, National Marine Fisheries Service, NOAA Seattle, WA	10. PROJECT/TASK NO.
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12. SPONSORING ORGANIZATION NAME AND ADDRESS National Marine Fisheries Service, NOAA Washington, DC 20402	13. TYPE OF REPORT AND PERIOD COVERED
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15. PUBLICATION REFERENCE

Experimental Exploitation of Competing Fish Populations - from Fishery Bulletin, Vol. 73, No. 4, 1975

16. ABSTRACT

Populations of the guppy, Poecilia reticulata, and the swordtail, Xiphophorus maculatus x X. helleri, were grown both independently and in competition under controlled conditions. Measures of recruitment were available as weights of juveniles returned to adult tanks from separate nursery tanks. Data from fitted curves showed that guppy recruitment exceeded that of the swordtail under both independent and competing conditions. Depression of recruitment by competition was greater in the swordtail than in the guppy. A mathematical model for competing populations consisted of a pair of differential equations including elements of the Volterra competition formulae and the Fox exponential surplus-yield model. By using the exploitation rates applied in the experiments, and constants from the independent populations, the model was applied to biomass data from the control pair of competing populations. Successive trials resulted in a reasonably good fit, and competition coefficients from this were used to fit data from the exploited test pair. Results from the experiments suggest that exploiting both members of a competing pair is preferable to exploiting either alone. (Author modified)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Fishing, *Fishing grounds, *Fisheries, *Exploitation, *Experimentation, Experimental data, Aquatic biology, Marine biology, Aquatic animals, Marine fishes, Sampling, Aquaculture, Animal behavior

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Experimental exploitation, *Fish populations, *Guppies, *Swordtails, *Fish competition, Fish experiments, Fish exploitations, Mathematical models, Fishery dynamics

17C. COSATI FIELD/GROUP

6C, 8A, 14B

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1. NOAA ACCESSION NUMBER
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3. RECIPIENT'S ACCESSION NUMBER
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4. TITLE AND SUBTITLE
Pheromonal Stimulation and Metabolite Inhibition of Ovulation in the Zebrafish, Brachydanio Rerio

5. REPORT DATE

6.

7. AUTHOR(S)
Lo-Chai Chen & Robert L. Martinich

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Department of Zoology,
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San Diego, CA 92182

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15. PUBLICATION REFERENCE
Pheromonal Stimulation and Metabolite Inhibition of Ovulation in the Zebrafish, Brachydanio Rerio - from Fishery Bulletin, Vol. 73, No. 4, 1975

16. ABSTRACT

Female zebrafish, Brachydanio rerio, would not ovulate in the absence of males in waters previously inhabited by the fish. Chemical presence of males and fresh, dechlorinated tap water each induced ovulation in about half of the trials. Application of the two factors in combination gave 100% ovulation. These results suggest that in the zebrafish a pheromone released by the males stimulates ovulation and that metabolites produced by the fish repress ovulation. It is postulated that metabolites restrict spawning of the fish to the rainy season and that the pheromone functions in synchronizing reproductive readiness between sexes or in conserving courtship energy expenditure. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Reproductive system, Sex glands, Marine fishes, Aquatic animals, Fresh water fishes, Aquaculture, Eggs, Experimental data, Sampling, Animal behavior, Vertebrates

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Pheromonal stimulation, *Metabolite inhibition, *Fish ovulation, *Zebrafish, *Brachydanio rerio, *Female zebrafish, Pheromone, Fish spawning, Fish reproduction, Egg fertilization, Fish reproduction

17C. COSATI FIELD/GROUP

6C, 8A

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1. NOAA ACCESSION NUMBER NOAA-75122301-17	2.	3. RECIPIENT'S ACCESSION NUMBER PB248 861-04-17

4. TITLE AND SUBTITLE Activity, Movements, and Feeding Behavior of the Cunner, *Tautogolabrus Adspersus*, and Comparison of Food Habits With Young Tautog, *Tautoga Onitis*, Off Long Island, New York	5. REPORT DATE
	6.
7. AUTHOR(S) Bori L. Olla, Allen J. Bejda, and A. Dale Martin	8. REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS Middle Atlantic Coastal Fisheries Center, Sandy Hook Laboratory, National Marine Fisheries Service, NOAA Highlands, NJ 07732	10. PROJECT/TASK NO.
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12. SPONSORING ORGANIZATION NAME AND ADDRESS U.S. Atomic Energy Commission	13. TYPE OF REPORT AND PERIOD COVERED
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15. PUBLICATION REFERENCE Activity, Movements, and Feeding Behavior of the Cunner, *Tautogolabrus Adspersus*, and Comparison of Food Habits With Young Tautog, *Tautoga Onitis*, Off Long Island, New York - from Fishery Bulletin, Vol. 73, No. 4, 1975

16. ABSTRACT

Field observations off Long Island, N.Y., using scuba and ultrasonic tracking, showed the cunner, *Tautogolabrus adspersus*, to be active during the day and inactively lying in shelter at night. Fish restricted their movements during the day, remaining within 2 m of the structure providing the nighttime shelter. The fish overwinter within their home territory in a torpid, nonfeeding state. Cunner fed primarily on invertebrates, foraging both benthically and in the water column. Competition between cunner and young tautog, *Tautoga onitis*, for *Mytilus edulis* was apparent during May-June when it is the major food item for both species. But beginning in July and extending through October, while tautog continued to feed primarily on mussels, cunner shifted to a diet consisting mainly of the isopod, *Idotea baitica*. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Food habits, *Animal nutrition, *Animal behavior, *Marine fishes, Aquatic animals, Sampling, Fishing, Fishing grounds, Oceans, Aquaculture, Vertebrates, Invertebrates

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Fishery Bulletin, *Cunner, *Tautogolabrus adspersus,*Tautoga onitis, *Young tautog, *Fish food habits, *Fish feeding, Fish movements, Fish activity, Fish studies, Temperate water fishes

17C. COSATI FIELD/GROUP

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1. NOAA ACCESSION NUMBER NOAA-75122301-18	2.	3. RECIPIENT'S ACCESSION NUMBER PB248 861-04-18

4. TITLE AND SUBTITLE
Correlation of Upwelling Index and Dungeness Crab Catch

5. REPORT DATE

6.

7. AUTHOR(S)
Louis W. Botsford and Daniel E. Wickham

8. REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Bodega Marine Laboratory,
P.O. Box 247,
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10. PROJECT/TASK NO.

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15. PUBLICATION REFERENCE
Correlation of Upwelling Index and Dungeness Crab Catch - from Fishery Bulletin, Vol. 73, No. 4, 1975

16. ABSTRACT

The statistical relationship between upwelling intensity and the annual _Cancer_ _magister_ catch is examined using techniques of time series analysis. The statistical relationships between upwelling in different years and crab catch in different years are examined. The statistic used is the correlation coefficient for varying time lag. The results correlating upwelling and crab catch indicate that time lag is short enough to demonstrate that adults are affected, and that the time lag is shorter in California than in Oregon or Washington. The crab catches appear to be cyclic with a period of 9 yr in California and 12 yr in Washington and Oregon. Possible causal mechanisms for the statistical relationships are presented. Results suggest that variations in crab catches may be due primarily to biological rather than abiotic influences. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Crabs, *Upwelling, *Ocean currents, *Arthropoda, *Crustacea, *Shellfish, *Dissolved organic matter, Fishes, Fishing, Fishing grounds, Fisheries, Oceans, Seafood, Sampling, Aquatic animals, Aquaculture

17B. IDENTIFIERS/OPEN-ENDED TERMS

*Dungeness crabs, *Crab catch, *Crab landings, *Upwelling index, *Upwelling intensity, Abiotic influences, Lag differences, Crab studies, Upwelling studies, Crab fishing, Fishing catches, Fishing predictions

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16. ABSTRACT

In an investigation of net feeding, 11 species of fish (5 gonostomatids, 6 myctophids) captured in a double-net Tucker trawl were examined. Stomach contents of fish retained by a coarse mesh "fish-catcher" in one net were compared to contents of fish which had accumulated with plankton in the cod end of the adjacent net. Out of 19 species-collection pairs (700 fish), there were significant ($P<0.05$) differences in number of prey items in stomachs of only three species in five collections. Two pairs, fish from the cod end and in three pairs, those from the "fish-catcher". contained significantly more prey than fish from the adjacent trawl. There were little or no significant differences between trawls in number of fish scales, prey diversity, or prey size. These results suggest that literature data on diet of mesopelagic fishes is not heavily biased from net feeding and that existing collections can be used for feeding investigations. (Author)

17. KEY WORDS AND DOCUMENT ANALYSIS

17A. DESCRIPTORS

*Fishes, *Plankton, *Nets, *Fishing, Sampling, Zooplankton, Taxonomy, Food chains, Food habits, Animal behavior, Sampling, Fisheries, Animal nutrition

17B. IDENTIFIERS/OPEN-ENDED TERMS

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MARINE TROPHIC INTERACTIONS BY DYNAMIC SIMULATION OF FISH SPECIES

JAMES D. PARRISH[1]

ABSTRACT

A mathematical model was developed for performing dynamic simulations of groups of interacting animal species. The energy balance of the individual animal was modeled so that growth and reproduction respond to food consumption after metabolic expenses are met. Populations change in response to recruitment (based on parental spawning) and mortality from natural causes, predation, starvation, and (where applicable) human exploitation. The forms of the various component mathematical functions were derived from the available ecological sources. Functions and parameters are especially applicable to marine fish species. Trophic webs of any size or form can be constructed using this basic species model. Computer solution of the essentially continuous differential model gives a time history of trophic and population variables for all species in the web.

Models of trophic webs of 2, 3, and 4 levels were constructed and exercised. These were used to examine effects of age class structure, reproductive time lag, and population regulation by starvation mortality and fecundity control. Competition between species and the effects of a top predator on competitors, with and without human exploitation, were studied.

Thus far in the history of trophic ecology there has been little effort to bring together the important results of the diverse studies which provide the components of the total trophic system into a construct that will permit analyzing the effects of metabolism, food consumption, reproductive effort, and the structure of the trophic web upon the weight, population, and biomass of the various species involved. Perhaps the most complete and useful approaches in the literature are those of Menshutkin and Kislyakov (1967, 1968), Menshutkin (1968), Menshutkin and Prikhodko (1968, 1969, 1970), Karpov et al. (1969), Krogius et al. (1969), Menshutkin and Umnov (1970), Lassiter and Hayne (1971). The present work is an attempt to create a complete model for fish in the natural environment and to employ it for the stated type of total trophic analysis.

The mathematical "trophic anatomy" of the generalized species modeled contains certain functions which represent trophic interactions with other species. The trophic web consists of an arbitrary number of such interacting species, coupled in this way into any arbitrary design; e.g., with any number of trophic "levels" (or coupled across levels), any number of species at each level, any number of predator species on a single prey species, etc. The trophic properties of the generalized, modular species are established by specifying a set of equations which define its various ecological functions, such as respiratory metabolism, feeding, natural mortality, and reproduction. The composite nature of the model species' trophic anatomy permits considerable structural flexibility in model development. A particular ecological function, such as feeding rate as a function of prey abundance, may be expressed differently in different simulation runs by changing a single component equation. The separate identity of each species is determined primarily by the numerical values of the parameters in its component functions, but the form of functions may be different in different species where the data dictate.

The model approach used allows a number of different levels of approximation. In the simulations performed here, no differentiation is made between sexes in the populations. The sexes could easily be represented separately at the cost of more computing time and a larger data base. A common and convenient simplification that is used in most of the present simulations is construction of an entire species population of identical individuals. Thus, the individual must be given a set of characteristics and parameter values that are in some sense representative of the entire life history after recruitment. A population with separate age classes has also been created explicitly with the present model.

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The model was employed in a number of simulations for a variety of trophic webs. There were not sufficient data at hand for all the species of a real trophic web to permit simulation of such a web in this way. The parameters and initial values used in these simulations are, therefore, reasonable illustrative values for fish in the natural environment, based mostly on the literature.

Despite the scarcity of the real data that would be required to use the model effectively for quantitative prediction of real systems at present, models of this sort have considerable immediate value. Representing and interrelating animal functions analytically enforces a discipline in thinking which tends to clarify perceptions of the trophic relations. Formulation of a system in mathematical functions makes clear the nature of the data required, so that effort in gathering data can be applied efficiently. Component functions for a single species can be collected from a variety of sources and fused. The trophic behavior of the resulting model species can be studied, at least qualitatively, to see if the model behaves as the animal appears to behave. If the species model appears to represent the animal reasonably well, and if a trophic web is constructed from such animals, some confidence may be placed in its predictions of the behavior of the real system—a system which may be much more difficult to evaluate independently of the model.

THE MODEL

The basic model used for each species in every trophic web was developed from an energy balance of the individual and a formulation of the population dynamics of the species. Table 1 contains a glossary of symbolic notation used in the model.

(A) The Energy Balance

The energy balance was written by equating assimilated food intake, kC, to the sum of the three physiological uses of the assimilated food: respiratory metabolism, Q, reproductive material produced for spawning, S, and growth, G.

$$kC = Q + S + G \tag{1}$$

Similar expressions are found in Winberg (1956:210, 1962), Ivlev (1961a), Warren and Davis (1967), Mann (1967, 1969), Davis and Warren (1971), and elsewhere. Mann (1965) has made one of the very few attempts to include the S term quantitatively in the balance. Most workers (e.g., Winberg 1956:209; Mann 1967, 1969) find that to a very acceptable ecological approximation, most fish under most circumstances assimilate a fairly constant fraction, $k \approx 0.8$, of the food, C, consumed (C, the feeding rate, is commonly called the ration and will be so designated herein). Ten (1967) should be consulted for a minority opinion on the effective constancy of k. Kostitzin (1939:180) and Beverton and Holt (1957:113) also deal with the form of possible variation.

All the above terms are time rates. In the present simulations, the time unit used is the year. Since G is dW/dt, the instantaneous value of body weight, W, can be found by integration of G. Each term in Equation (1) can be expressed as energy or as the equivalent weight of body tissue, wet (live) or dry. In these simulations, all terms for all species are expressed in wet weight of tissue, based on a standard conversion factor of 1 kcal/g wet weight (Winberg 1956; Mann 1969). Recent results (Davis 1968; Kausch 1968; Brett et al. 1969) on changes in water content of fish tissues at various nutritional states suggest that a dry weight basis may be noticeably more accurate where data are available. The use of different conversion factors for different species or conditions, when known, introduces no conceptual problems. That Equation (1) can be balanced using experimental values of k, C, Q, and G determined simultaneously in the laboratory for a group of fish over a range of sizes, ambient temperatures, and nutritional states, has been demonstrated by Kausch (1968), using the carp, *Cyprinus carpio*.

The results of many investigations indicate that respiratory metabolism can be expressed approximately as a function of body weight, W, by the relation

$$Q = \alpha W^{\gamma}, \tag{2}$$

where γ is some fractional power. For most fish species a value of $\gamma = 0.8$ appears to be sufficiently reliable for ecological purposes (Winberg 1956:149, 1962; Mann 1965, 1969; Paloheimo and Dickie 1966). Where a more accurate value of γ is known for a particular species, the model will accept it readily.

For the purpose of the present simulations, a level of α for a constant (or long-term average) temperature of 10°C is used. Based on a large

TABLE 1.–Glossary of symbolic notation used in the model. [Notation defined in referenced literature, when different from that of the present model, is not repeated here.]

Symbol	Definition
a	Numerical parameter in the Beverton and Holt reproductive function
B	Species biomass
B_i	Biomass of the *i*th species
B_1	Biomass of the food base
b	Numerical parameter in the Beverton and Holt reproductive function
C	Actual ration; actual rate of food consumption by an individual
C_{max}	Maximum ration when feeding to satiation
$Cp = Cp_{Total}$	Ration of a predator
Cp_i	Consumption of the *i*th prey species by a predator
c_{s1}	Numerical predation parameter in the linear feeding function
c_1	Instantaneous coefficient of natural increase of an "exponential growth" type food base
D_{FISH}	Rate of change of population due to fishing mortality
D_{NAT}	Rate of change of population due to natural mortality
D_{PRED}	Rate of change of population due to predatory mortality
D_{STARV}	Rate of change of population due to starvation mortality
E	Total egg production rate of a population
e	Base of natural logarithms
F	Coefficient of instantaneous fishing mortality
G	Actual growth rate of an individual
G_{max}	Maximum growth rate; growth rate when $C = C_{max}$
G_{VB}	Growth rate predicted by the von Bertalanffy growth function
g_m	Fraction of the species population that is sexually mature
g_1, g_2	Numerical parameters in the linear sexual maturity function for g_m
I_1	Constant of integration for critical starvation mortality time
j	Convenience combination of variables in Equation (A-2), Appendix
K_1	Recruit body weight coefficent
k	Ration assimilation coefficient; fraction of the ration assimilated
L_∞	Numerical parameter (theoretical maximum body length) in the von Bertalanffy growth function for length
M	Coefficient of instantaneous natural mortality
m	Numerical parameter in the starvation mortality function
m_{mc}	Numerical predation parameter in the Holling feeding function
N	Species population
N_{Fish}	Population of a fish species
N_i	Population of the *i*th species or age class
N_m	Sexually mature species population
N_0	Initial population
N_p	Predator population
N_s	Standard equilibrium value of species population
n	Numerical parameter in the starvation mortality function
P	Prey abundance
P_1	Rate of food base biomass input to the system in a "constant input" model
Q	Rate of respiratory metabolism of an individual
Q_{max}	Rate of respiratory metabolism of an individual at maximum ration
R	Rate of reproductive recruitment
R_s	Standard equilibrium recruitment rate
r	Fraction of the maximum ration actually consumed
S	Fecundity: actual rate of production of reproductive material by an individual
S_{max}	Maximum fecundity at current body weight
s	Computed numerical parameter in the starvation mortality function
t	Time
t_c	Critical time to 100% starvation mortality
u	Fecundity coefficient of an individual
v_i	Coefficient of predator preference for the *i*th prey
W	Body weight of an individual
W_{Fish}	Body weight of an individual fish
W_i	Body weight of an individual of the *i*th species or age class
W_0	Initial body weight of an individual
W_{prey}	Body weight of a prey individual
W_s	Standard equilibrium body weight of an individual
W_∞	Numerical parameter (theoretical maximum body weight) in the von Bertalanffy growth function
α	Respiratory metabolism coefficient
α_{max}	Respiratory metabolism coefficient at maximum ration
α_{starv}	Respiratory metabolism coefficient at zero ration
γ	Numerical parameter (weight exponent) in the respiratory metabolism function
κ	Numerical parameter in the von Bertalanffy growth function
ξ	Numerical predation parameter in the Ivlev feeding function

collection of data from the experimental literature, a level of α appropriate to an average spontaneous activity level was chosen. The instantaneous value of α is allowed to vary in response to ration according to the equation

$$\alpha = \alpha_{starv} + (\alpha_{max} - \alpha_{starv}) \frac{C}{C_{max}}, \qquad (3)$$

where C is the actual instantaneous ration, α_{starv} is the value corresponding to minimum metabolic rate at complete starvation, and α_{max} corresponds to the maximum metabolic rate when feeding to satiation at ration C_{max}. Equation (3) is a linear expression that generally approximates the best results from the few applicable long-term fish feeding and growth experiments (Davis and Warren 1965, 1971; Paloheimo and Dickie 1965, 1966; Beamish and Dickie 1967; Warren and Davis 1967; Brett et al. 1969). Use of Equation (3) in Equation (2) gives Q for any size fish at any feeding level.

Fecundity of fish must be dependent on size and, at least in some limiting sense, on nutrition. A number of workers have noted reduced fecundity in overcrowded, undernourished fish populations and have speculated on how this reduced fecundity might tend to regulate the population (Woodhead 1960; Nikolskii 1961, 1962; Scott 1962; Bagenal 1967; Mackay and Mann 1969). There is good evidence (Simpson 1951; Bagenal 1957, 1967; Beverton 1962; Pitt 1964; LeCren 1965; Bagenal and Braum 1971) that in most fish with adequate food supply above metabolic demands, fecundity is strongly dependent upon body weight. Regressions on weight usually fit better than regressions on length or age (Bagenal 1957, 1967; Nikolskii 1962). It seems reasonable to represent the rate of production of reproductive material, S, (or accumulation of body stores for that purpose) as a simple function of weight. Although more general functions have been proposed (Bagenal and Braum 1971), apparently most regressions so far fitted using data from specimens have been quite close to the linear expression.

$$S = uW, \qquad (4)$$

where u is a constant. In the present simulations, $u = 0.1$ in all cases, based on average values for several species and both sexes (Bagenal 1957, 1967; LeCren 1958, 1962; Mann 1965; Norden 1967; Phillips 1969). The linear function is truncated near its lower end at a weight corresponding to sexual maturity. This is consistent with the general observation that the onset of sexual maturity in fish appears to be a function of size rather than age (Beverton and Holt 1959; LeCren 1965). Exceptions for individual species are noted in Bagenal (1957).

Trophic factors regulate the animal's fecundity through their effect on body weight. Also, when food intake becomes sufficiently low, there must not be enough energy above metabolic demands for normal fecundity. The scanty field data available suggest that usually fish sacrifice growth for reproduction, so that as food intake decreases, fecundity stays at or near normal (with decreased growth) until the net energy above metabolic expenditures is less than the normal fecundity requirements, after which fecundity decreases (Mackay and Mann 1969). The model operates in this way.

The ration, C, under any instantaneous set of conditions, is obtained from the maximum ration, C_{max}, and the current abundance of the prey which constitutes the food supply. C_{max} is dependent on body weight, and its current value can be determined from Equation (1) if the maximum growth rate, G_{max}, is known. Since G_{max} is a function of the current size of the individual, this function is required. Data from appropriate ad libitum feeding experiments with a particular species of interest could be fitted to the appropriate function to give continuous values of G_{max}. The von Bertalanffy growth function is a convenient one to which growth data from a large number of fish species have been fitted (e.g., Beverton and Holt 1959; Ursin 1967). In its differential form it expresses growth

$$G_{VB} = \kappa(W_\infty{}^{1/3}W^{2/3} - W), \qquad (5)$$

where κ and W_∞ are numerical fitting parameters (κ corresponds to the ${}_1k$ of Ursin 1967, and to 3 times the K of Beverton and Holt 1959). W_∞ corresponds to a theoretical maximum weight, asymptotically approached. Values of κ and W_∞ for the present simulations are taken for certain illustrative species from Beverton and Holt (1959) and Ursin (1967:2421-2423). Equation (5) is employed in the model with a constant coefficient of 4.0 as an arbitrary standard adjustment to represent the highest feeding conditions. This gives a relationship between values over the full feeding range (e.g., zero, maintenance, and maximum ration) consistent with those observed in long-term feeding and growth experiments. With the C_{max} term thus expressed, the Q_{max} term is simply Equation (2) with $\alpha = \alpha_{max}$ and using the current weight, W. The S_{max} term comes from Equation (4). Thus

$$C_{max} = \frac{Q_{max} + S_{max} + G_{max}}{k}. \qquad (6)$$

There is a considerable and developing body of theory, for which evidence continues to accumulate, that where environmental conditions are fairly stable, a predator's ration may be expressed as a fraction, r, of its maximum ration, r being a simple function of the abundance of prey, P. This approach is taken as a useful long-term ecological approximation, in which short-term behavioral factors, factors affecting the accessibility of the prey, etc. are smoothed out. Several expressions for this relationship have been proposed.

Three alternative expressions for simple predation with no explicit competitive effect between predator individuals were used in the model in different simulation runs. These are:

Linear: $r = c_{a1}P$ (7A)
Ivlev: $r = 1 - e^{-\xi P}$ (Ivlev 1961b) (7B)
Holling: $r = \dfrac{P}{m_{mc} + P}$ (Holling 1959) (7C)

where c_{s1}, ξ, m_{mc} are numerical parameters. For prey species modeled as described here, expressing P in terms of prey numbers rather than biomass seems to have system stability advantages. It is through Equation (7) that this species interacts with the next lower species in the trophic chain (web).

The instantaneous rate of production of reproductive material and growth at the current body weight and prey abundance can be determined by use of the above terms in Equation (1). Using $r = \frac{C}{C_{\max}}$ from Equation (7) in Equation (3) gives the current value of α to be used in Equation (2) to give the current value of Q. When food supply is adequate; i.e., when $kC - Q > S_{\max}$, "fecundity" is

$$S = S_{\max},$$

and, from Equation (1), positive growth is

$$\frac{dW}{dt} = G = kC - Q - S_{\max}. \tag{8}$$

When food supply is so low that $0 < kC - Q < S_{\max}$, growth is zero and fecundity is

$$S = kC - Q. \tag{9}$$

In more extreme food shortage, when $kC - Q < 0$, fecundity is zero and growth is

$$\frac{dW}{dt} = G = kC - Q. \tag{10}$$

(Note that in the last case, growth is negative; i.e., dystrophy occurs). Equations (8) and (10) are in differential form, representing rates of change of body weight. Numerical integration of these equations gives "continuous" values of body weight over the entire time span of the simulations. Figure 1 shows the relationships between the component equations which describe a single species.

(B) Population Dynamics

Numerical changes in the population of any species are the net result of gains through reproduction (recruitment) and losses through the various sources of mortality. Therefore, the dynamics of any species population can be summarized in the expression

$$\frac{dN}{dt} = R + D_{\text{NAT}} + D_{\text{PRED}} + D_{\text{STARV}}. \tag{11}$$

The rate of change of population is the algebraic sum of four terms: reproductive recruitment, R, natural mortality, D_{NAT}, mortality due to predation, D_{PRED}, and starvation mortality, D_{STARV} (the sign of the reproductive term is positive; all the other terms have negative signs). Equation (11) is used in essentially this form for the representative individual model. For the age class model, the last three terms appear for all age classes. Instead of including the first term, the appropriate number of recruits is simply introduced as a pulse into the youngest age class at the appropriate times in the simulation.

The recruitment rate, R, is expressed as a function of the rate of egg production, E, by the Beverton and Holt (1957:49) reproductive function

$$R = \frac{1}{a + \frac{b}{E}}, \tag{12}$$

where a and b are numerical parameters. A simple relationship such as Equation (12) is appropriate for the present model where the response of a system of essentially adult populations to purely trophic variables is of interest. The egg production rate, E, is the cumulative spawn of the entire mature population, N_m; i.e.,

$$E = N_m S. \tag{13}$$

For the age class model, this involves summing over all mature age classes and over the entire year. All real species have some reproductive time lag or "generation time." In all except the simplest animals, this lag is significant and can have important influence on the dynamics of the population. Such lags of any desired length are introduced in the simulations by properly coding the programs so that the E produced in 1 yr is stored and used in Equation (12) to compute the R for the appropriate later year.

Except for fishing mortality, natural mortality is the only kind expressed in most fishery models. The position taken is that all mortality not due to fishing is "natural" and may be measurable in an unexploited stock or by eliminating the fishing mortality from statistics on an exploited stock by some analytical technique. Thus defined, natural mortality is almost invariably represented in

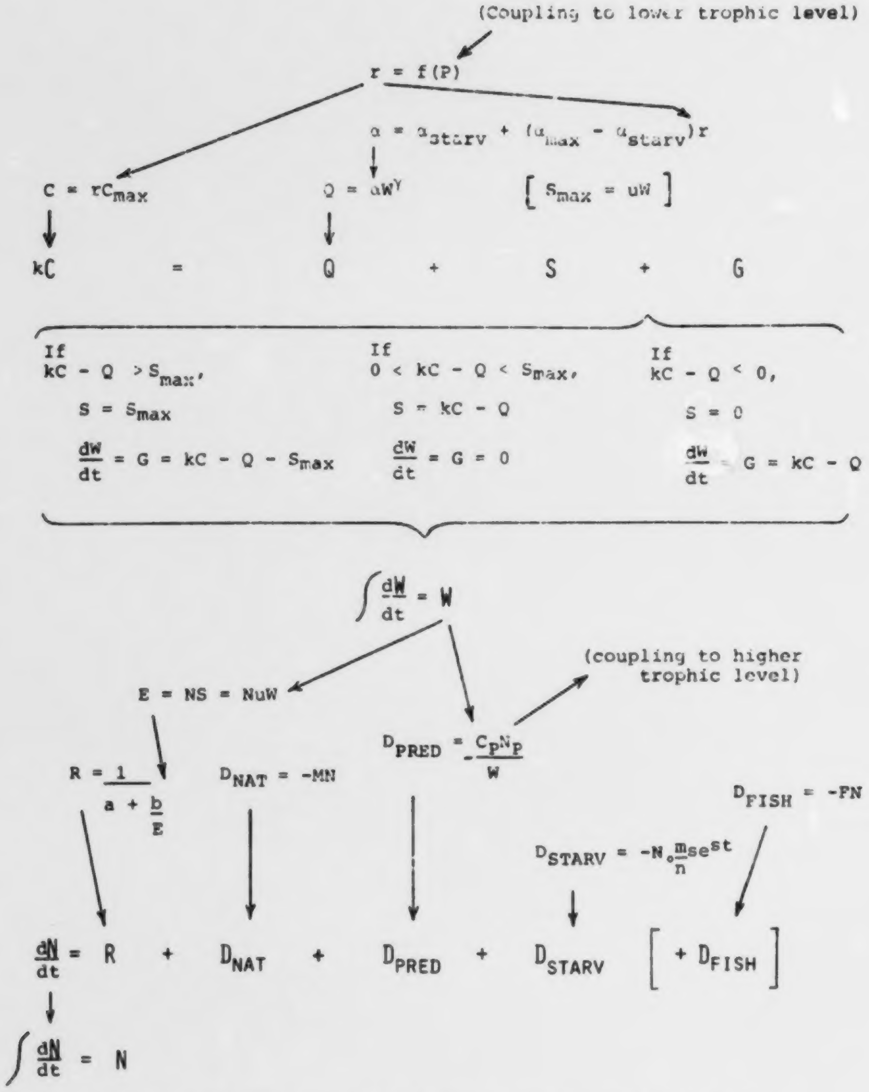
(Coupling to lower trophic level)
r = f(P)
α = α_starv + (α_max − α_starv)r
C = rC_max
Q = αW^γ
[S_max = uW]
kC = Q + S + G
If kC − Q > S_max, S = S_max, dW/dt = G = kC − Q − S_max
If 0 < kC − Q < S_max, S = kC − Q, dW/dt = G = 0
If kC − Q < 0, S = 0, dW/dt = G = kC − Q
∫ dW/dt = W
E = NS = NuW
(coupling to higher trophic level)
R = 1/(a + b/E)
D_NAT = −MN
D_PRED = −C_P N_P / W
D_FISH = −FN
D_STARV = −N_o (m/n) se^st
dN/dt = R + D_NAT + D_PRED + D_STARV [+ D_FISH]
∫ dN/dt = N

FIGURE 1.–Relationships between principal component equations describing a single species.

fishery works by the simple decaying exponential function

$$D_{\mathrm{NAT}} = -MN, \tag{14}$$

where M is a numerical parameter, the "coefficient of instantaneous natural mortality." The function has been applied very widely, whatever the predation rate may be (even where it is zero) and in situations where starvation probably does not occur. Lacking data to support another assumption, it seems reasonable to use Equation (14) to express the more limited category of natural mortality of the present model also. In the model, then, natural mortality is all mortality not due to predation or starvation (the trophic controls) or fishing, and would include death due to disease, senility, accident, environmental stress, etc. Field data for this limited class of mortality are rather scarce. For the hypothetical species in these simulations, approximate conventional M values were taken from Beverton and Holt's (1959) tables, and for species under predation, these were at times modified. In the age class models, different values of M are used for different age classes. Beverton and Holt (1959) discussed the variation of mortality with age more fully.

The expression for mortality due to predation, D_{PRED}, comes directly from the ration of the predator species, C_P, modeled as described in the preceding discussion of energy balance. Thus, the rate of change of prey population due to predation, D_{PRED}, is

$$D_{\mathrm{PRED}} = -\sum \frac{C_P N_P}{W_{\mathrm{prey}}}, \qquad (15)$$

where N_P is the number of predators, each with ration, C_P, W_{prey} is the weight of a prey individual, and the summation is over all predator species which consume the particular prey. Equations (15) and (7) provide the coupling between each model species and the other species with which it interacts in the trophic web.

Despite the scarcity of knowledge on starvation in fish, it would seem that a complete model for a system controlled by trophic variables should include some reasonable attempt at a formulation of this source of mortality. An expression was developed that can approximate the general form of the survival versus time curves from Ivlev's (1961b:266) starvation experiments with fish. This expression states that under pressure of starvation alone, the surviving number, N, of an initial population, N_0, after time, t, will be

$$N = N_0 \frac{1}{n}(m + n - me^{st}). \qquad (16)$$

The m and n are numerical parameters, and the parameter, s, comes from the boundary condition at 100% mortality, after the critical time, t_c, to extinction has been found from the integrated form of the energy balance equation under starvation conditions (see Appendix). The form of the function of Equation (16) is plotted in Figure 2. Use of Equation (1) in computing t_c and s provides an appropriate curve for any ration. The model uses the differential form of Equation (16),

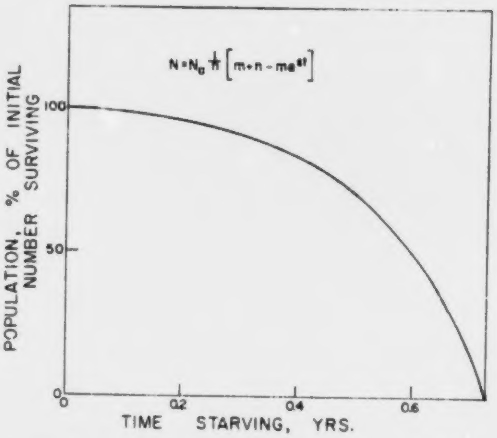

FIGURE 2.–Survival curve of a population undergoing only starvation mortality at zero ration.

$$D_{\mathrm{STARV}} = -N_0 \frac{m}{n} s e^{st}, \qquad (17)$$

as the fourth term in Equation (11).

When exploitation by man is included in the system, the only modification is the addition of another term to Equation (11). In accordance with conventional fishery theory and the concept of chance encounter between fish and fishing gear, this term is exactly like Equation (14); i.e., fishing mortality, D_{FISH}, is

$$D_{\mathrm{FISH}} = -FN. \qquad (18)$$

The numerical parameter, F, is an expression of the intensity of fishing effort and the vulnerability of the prey to the fishing gear.

Equations (12), (14), (15), (17)–and (18) where appropriate–provide all the terms for determining rate of change of population from Equation (11). (Figure 1 summarizes their relationships.) Numerical integration of Equation (11)–less the first term for the age class model–gives "continuous" values of population of the species over the entire time span of the simulation. Biomass of an entire species population at any instant is the product of instantaneous values of W and N (summation of a group of such products in age class models). Production over any desired period is obtained by integrating the incremental growth rates, G, and reproductive products, S (if desired), over that period.

(C) The Trophic Web

All the fish species in a trophic web can be modeled more or less as described above. Many invertebrates that serve as fish food can be modeled in much the same way, with some appropriate changes in individual component functions and by use of the proper parameter values (see Winberg 1962, and Mann 1969 for discussion relative to invertebrates). Since this model uses feeding functions based on prey abundance, an operational limitation is imposed that the ultimate resource base–the lowest item in the food chain–cannot be modeled fully in this way. In terms of total ecosystems, this is natural enough. Although the ultimate autotroph might be thought to "prey" upon inorganic nutrients, and models for plant growth as a function of nutrient abundance exist, the present model is obviously not appropriate for autotrophs.

Thus, any trophic web modeled in this way must have at its base an arbitrarily defined species or group of species. The purpose of this first exercise with the model is to explore trophic interactions among fishes. Therefore, the cause of clarity seems best served by modeling all the species of interest as fishes. The level(s) below the lowest fish species–the food base for the fish community–is then given only the simplest representation.

Two types of food base have been used in these simulations: 1) the "constant input", and 2) the "exponential growth." Properties of the constant input base are that biomass, B_1, enters the system at a constant rate, P_1, and is reduced only through predation by the higher level, fully modeled species. Thus, the rate of change of food base biomass is

$$\frac{dB_1}{dt} = P_1 - \Sigma C_P N_P, \qquad (19)$$

where the summation is over all predators with their individual rations, C_P, and populations, N_P. Ecologically, this system might correspond to a fish community whose base prey enters the community feeding area at a constant rate; e.g., as brought in by water circulation or by migration as prey individuals continuously reach a particular life stage. Because of its extreme simplicity, this type food base model is preferred for studying the trophic relationships of fishes higher in the web.

Properties of the exponential growth food base are that biomass is produced at a rate directly proportional to the current standing crop of biomass and is reduced only through predation by the higher level species. Thus

$$\frac{dB_1}{d_t} = c_1 B_1 - \Sigma C_P N_P, \qquad (20)$$

where c_1 is a numerical parameter corresponding to the "instantaneous coefficient of natural increase" of classical population growth theory. Again the summation is over all predator species preying on the food base. Without predation, B_1 would of course increase exponentially and indefinitely. This makes stability of such a system precarious, a fact borne out by experimentation with the model.

For these simulations, numerical values of P_1 and c_1 were selected arbitrarily to be compatible with the standard equilibrium state of the trophic webs constructed.

SIMULATION TECHNIQUE

Combination of the previously described functions produces the basic species model. A single such model species, with one of the food base models described above as prey, was exercised over a range of conditions and with some variety in certain component functions, in an effort to become familiar with some of the dynamic properties of the basic species model. Groups of such model species were then interconnected in various ways to explore the behavior of various trophic webs. Interactions between species occur through Equations (7) and (15). Where a predator feeds on more than one prey species, P in Equation (7) for that predator is the total abundance of all the n species. For each of the n prey species, the predation mortality imposed by that predator is given by Equation (15) in which the C_P upon the ith prey is

$$C_{P_i} = C_{P_{\mathrm{TOTAL}}} \frac{v_i N_i}{\sum^{n} v_i N_i}, \qquad (21)$$

where N_i is the current population of the ith species, and v_i is a coefficient expressing predator preference and availability (vulnerability) of the prey. The two (or more) elements contained in v can be separately expressed by making v a product of separate coefficients. By Equation (21), the predator tends to adjust the makeup of its diet proportionately to the abundance of the various prey, but bias is allowed for known preferences or differences in the ease with which various prey can be taken. These features, together with the basic structure of the age class model, allow that predators and prey interacting with any species may be different for different age classes of the species or may change in their degree of importance.

All the model species created for these simulations are hypothetical. To avoid resorting to pure fantasy and to get some consistency among certain species properties, each model fish species was based on a real fish species (see Table 2). Real species were selected which are sympatric, and in fact, each of the predator/prey relationships modeled has been reported in the literature in a nonquantitative way. A major simplification in

TABLE 2.–Values of parameters and of basic variables at standard equilibrium state as used in simulations. [Values shown in parentheses are alternate values used in some simulations.]

Parameter or standard equilibrium variable	Units	Source	Namesake species				
			Clupea sprattus	*Clupea sprattus*	*Clupea sprattus*	*Scomber scombrus*	*Sarda sarde*
			Model species				
			E	A	B	C	D
α_{starv}	$g^{0.2}$-$yr^{-1.0}$	See MODEL section (A)	1.0	1.0	0.7	1.0	1.0
α_{max}	$g^{0.2}$-$yr^{-1.0}$		7.0	7.0	4.9	7.0	7.0
u	yr^{-1}	See MODEL section (A)	0.1	0.1	0.1	0.1	0.1
γ		See MODEL section (A)	0.8	0.8	0.8	0.8	0.8
k		See MODEL section (A)	0.8	0.8	0.8	0.8	0.8
K	yr^{-1}	Ursin (1967): 2421-2423	1.75	1.75	1.75	1.2	0.530
W_{∞}	g	Ursin (1967): 2421-2423	30.6	30.6	30.6	516.0	9,400.0
M	yr^{-1}	Beverton and Holt (1959)	1.0	1.076 [0.1169]	1.076 [0.1169]	0.9 [0.0325]	0.9
W_s^*	g		10.0	15.16106	15.16106	150.0	600.0
N_s^*			1.0×10^5	0.61032×10^5 (1.22064×10^5)	0.61032×10^5 (1.22064×10^5)	5,000	500
R_s^*			1.0×10^5	0.65680×10^5 (1.31360×10^5)	0.65680×10^5 (1.31360×10^5)	4,500	450
a		Computed based on R_s	0.66667×10^{-5}	1.09232×10^{-5} (0.54616×10^{-5})	1.09232×10^{-5} $(0.54616 \times 10^{-5}$	0.13333×10^{-3}	0.13333×10^{-2}
b	g-yr^{-1}	Computed based on R_s	0.33333	0.39806	0.39806	6.66667	26.66667
ζ		See SIMULATION TECHNIQUE section.	0.49584×10^{-7}	0.60178×10^{-7}	0.60178×10^{-7}	0.37902×10^{-6}	0.79657×10^{-4}
c_{sl}				0.45217×10^{-7}	0.45217×10^{-7}	3.03435×10^{-6}	0.65706×10^{-4}
m_{mc}				1.21158×10^7	1.21158×10^7	0.20750×10^6	0.10219×10^5
m		Selected to fit form of Ivlev (1961b: 266)	1.0	1.0	1.0	1.0	1.0
n			40.0	40.0	40.0	40.0	40.0
v		See SIMULATION TECHNIQUE section		1.0	1.0		
g_1		See RESULTS section (A)		−1.02147	−1.02147	−1.00000	−0.71428
g_2	g^{-1}	See RESULTS section (A)		0.13333	0.13333	0.013333	0.00286
r	yr^{-1}	See RESULTS section (D)		0.05 to 0.90	0.05 to 0.90	0.05 to 0.20	

*Values of variables at standard equilibrium state.

the simulations is the extremely limited range of diet of the model species; their factual namesakes have rather catholic tastes.

For these hypothetical species, a set of values for an arbitrary standard equilibrium condition was established as follows. Populations for all species were arbitrarily set at values that seemed reasonable relative to each other and in respect to the various body weights and reproductive rates. Using the various parameters selected, for each species, the r value corresponding to the standard equilibrium state was then computed. From this r and the equilibrium population of the prey, the predation parameters of Equation (7) were computed. Using this procedure for each fish species, working up the trophic chain, a complete set of equilibrium values for all species became available. A compatible trophic web was thus created arbitrarily, having at least static stability; i.e., dN/dt and dW/dt were zero for all species. Table 2 provides the values of parameters and of basic variables at standard equilibrium state for the model species used in these simulations. Where a consistent set of laboratory and field data on species in a real trophic web were available to be used in the model for predictive purposes, some of these procedures would be unnecessary.

Like all simulations, those run with the model require that initial conditions be specified. Typically in these runs, the initial conditions were those of the standard equilibrium state with the exception of some single variable value which was displaced so as to perturb the system. For example, a simulation run started with all variables at equilibrium except B_1 might be analogous to the natural occurrence of sudden catastrophic mortality in a prey species. Initial conditions are discussed further under RESULTS. In each case, the simulation was allowed to run for an arbitrary length of time, or until automatically terminated when some variable reached a prescribed limiting value. Usually runs were continued until a stable state (the original standard equilibrium or otherwise) was approached, or until a distinct monotonic trend with a predictable outcome was detected.

All the simulations were programmed using the IBM[2] System/360 CSMP (Continuous System Modeling Program) (International Business Machines Corporation 1969, 1971) and run on an IBM 360/50 Data Processing System.

RESULTS

A limitation of the approach taken here, as with any simulation model for numerical solution, is that mathematically exact and general solutions are not obtainable. A full solution of the system represents a very complex multidimensional response surface. In the very simplest case of one modeled fish species and a food base species, there are three basic dependent variables whose integrated values appear in the solution; viz., N_{Fish}, W_{Fish}, and B_1. In a "representative individual" model with n fish species and the food base, there are $2n + 1$ basic dependent variables, and in a similar model with x explicit age classes per species, there are $2nx + 1$ basic dependent variables.

A system with the complexity and nonlinearities of this type of model is capable of behaving quite differently in different regions of the state space. Since it is impossible to explore the entire response surface thoroughly, measures must be taken to limit simulation effort to regions of interest. Eventually a detailed and systematic exploration of regions of known interest using established optimization techniques (e.g., Box et al. 1953; Box 1954; Box and Hunter 1957) may be useful with the model.

For the present, the scope of simulation effort has been limited by selecting parameter values that seem reasonable and compatible for each of a small group of rather common fish species and by building out from a system already investigated to a larger system of which the original is a subset. In a number of cases where moderate changes to values of parameters or even to the form of component functions have been made, system dynamics have been somewhat altered or the system has even moved toward a new stable state. Usually, however, in a system with any regulatory capacity (stability) at all, the change has not been drastic. Rather large perturbations in initial values of the basic dependent trophic variables of such a system have not usually displaced the system to a distant stable region or resulted in breaking the trophic web (eliminating one or more species). This behavior of most of the systems simulated gives evidence that there is at least one region of some useful size in the total state space—i.e., the region in which the arbitrary equilibrium state has been placed—in which the system models are fairly stable. For these reasons, it is believed that the basic form of the behavior of systems demonstrated in these simulations has some generality beyond the specific cases tested. However, in all cases, the results shown here are simply examples of interest from an infinite number of possibilities.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The simulation technique used here is amenable to use in sensitivity analyses; i.e., for determination by a systematic program of successive trials how sensitive the result is to the numerical value of a parameter or an initial variable value. Such analyses not only help define useful regions for particular results; they also give an indication of how accurately particular parameters must be measured in the field or laboratory, so that effort is applied where it is important to the system result.

In describing the following results, the shorthand notation used to reference the trophic webs has the following form:

$$\text{P}\quad \underbrace{\begin{matrix}1 & 2 & 1 & 0 & 0\\ \text{1st} & \text{2nd} & \text{3rd} & \text{4th} & \text{5th}\end{matrix}}_{\text{Trophic level}}$$

The digit in each column indicates the number of species at that trophic level. Where two species appear at a common level, they compete for prey at the next lower trophic level and are preyed upon equally by the next higher trophic level. The lowest level is always occupied by the food base with biomass B_1.

(A) Regulation of Body Weight and Population

The basic species model seems to have a considerable capacity for self-regulation; i.e., it can return to an equilibrium state after sizable displacements of some of the variables in the system. The return usually involves a series of oscillations above and below the equilibrium values, with the degree of damping depending on the exact structure and parameter values.

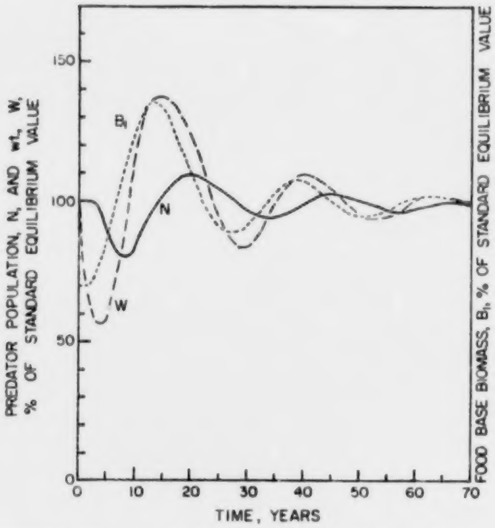

FIGURE 3.—Response of a single species to an initial perturbation in the abundance of its prey. N = predator population; W = predator body weight; B_1 = prey (food base) biomass.

One of the most common and interesting perturbations involves displacement of prey abundance. Figure 3 illustrates a P11000 trophic web with a representative individual model of a species A fish preying on an exponential growth type food base with an Ivlev feeding function. The system responded to an initial condition in which the fish population was at the standard equilibrium value and the prey abundance was initially about 71.4% of the standard equilibrium value. The system returned to the standard equilibrium state with damped oscillations. The purely population controls, natural mortality and reproduction (D_{NAT} vs. R), were satisfied initially, but the system was unbalanced trophically because of the scarcity of prey. Regulation resulted from the response of body weight and resulting fecundity to food consumption, balanced by natural mortality responding to the changing population level.

Similar stable responses were demonstrated with the model for cases of initial perturbation due to high prey abundance, B_1, high predator population, N, and high predator body weight, W.

At sufficiently low values of prey abundance and production, substantial starvation mortality can occur. This is particularly true when the prey abundance decreases suddenly, since the normal population response of the predator through reduced fecundity is delayed by the reproductive time lag. Figure 4 shows such mortality for a population for four age classes modeled explicitly. The abundance of each year class decreased with time until those which had become 4-yr-olds were decimated at about 1.6 yr after the start. The

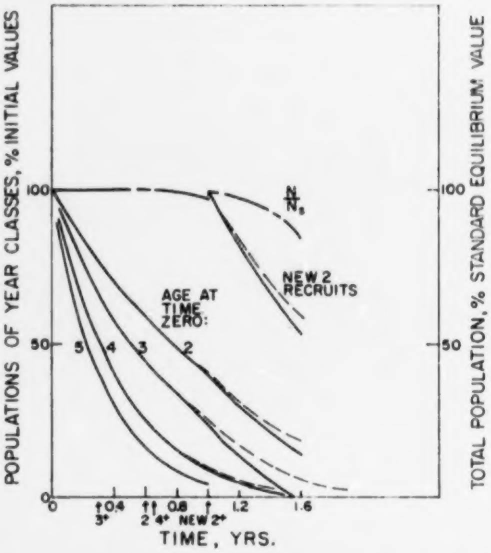

FIGURE 4.–Effects of starvation mortality on the 4 age classes of a species population and on the total population. A new class of recruits entered one year after the start of the simulation. Arrows indicate when starvation mortality began for each year class. (—— actual population of an age class; — — — population of an age class in the absence of starvation mortality; — - — N/N_{s}, where N = total species population, N_s = standard equilibrium value of total species population.)

dashed lines indicate the course of natural mortality. As interesting as the fate of individual year classes is the substantial effect on the total population (shown by the upper broken line in Figure 4).

Theoretically, starvation mortality should be capable of regulating the population. However, based on a considerable range of simulation runs, it appears that with the usual sets of reasonable parameter values for the species considered here, body weight and fecundity normally respond to produce regulation so that a starvation condition is not reached. With longlived, slowly growing species, starvation would tend to become a more important factor. In some of the cases simulated, where trophic conditions were sufficiently extreme to produce heavy starvation mortality, total extinction occurred. Figure 4 represents such a case, in which the food base biomass, B_1, was initially 20% of the standard equilibrium value and c_1 was 10%. Extinction occurred during the initial 2-yr reproductive time lag before fecundity changes could be reflected in recruitment. Some simulations were run in which fecundity was made unresponsive to actual body weight so that the effects of starvation could be better observed. With the nutritional control on fecundity thus removed, starvation occurred for some systems and started with B_1 at 50% of standard equilibrium and c_1 at 90%. With normal nutritional control on fecundity, these systems had survived.

Experience with the model indicates that for the types of species used, where extreme trophic conditions exist, disruption of the system is more likely to result from excessive stunting of growth and resultant failure of spawning than from starvation mortality. In age class models, the stunting can be observed directly in the failure of individuals of a year class to grow normally while in the recruited population. Where food supply is extremely low, actual weight loss by an individual can also be observed. In representative individual models, these separate effects are combined in the single continuous variable, W. A smaller-than-standard W represents a population that, on the whole, is undersize. If the population as a whole becomes sufficiently stunted, at some point, egg production will be reduced to zero. This corresponds to a population unable to reach sexual maturity. If the entire population fails to spawn for enough successive years, extinction of the local species population must result. It is difficult to see how a species could persist if it failed to spawn for a continuous period as long as its lifespan.

In most of the results shown here, no effort has been made to impose a sexual maturity limit on fecundity; i.e., Equations (4) and (13) with $N_m = N$ determine the egg production, E, at any body weight.

$$E = N_m u W = N u W. \qquad (22)$$

For exploring the limits of stability of systems against perturbations, it seems useful to represent the attainment of sexual maturity in the model. A "knife-edge" representation–one in which fecundity has a substantial positive value or functional form above some age, length or weight, and zero below it–has been used for simplicity in much fishery work. This may be a justifiable approximation of nature for some species, especially those with short lives, fast growth, and infrequent spawning. However, a smoother and more realistic representation seems desirable. For some species, data exist on the fraction of all individuals mature as a function of age, length, or weight. In some cases (e.g., Bagenal 1957) the weight function appears reasonably linear. This means that in Equations (13) and (22) the mature spawning population, N_m, can be expressed as

$$N_m = g_m N, \tag{23}$$

and

$$g_m = g_1 + g_2 W, \tag{24}$$

where g_1 and g_2 are numerical parameters, for all values of W between that which gives $g_m = 0$ and that which gives $g_m = 1.0$. At lower and higher values of W, g_m is 0 and 1.0 respectively.

For species A and C, information from Bigelow and Schroeder (1953) permitted a rough fitting of this function. The length corresponding to the body weight at which all were mature agreed reasonably well with the ratio: length at maturity/theoretical maximum length (L_∞) of Beverton and Holt (1959) for both species. The same sort of weight limits for the function were assumed for species D, in the absence of better data. The standard equilibrium weight and the 100% sexual maturity weight were made to coincide in each species. This means that in this particular modified model, any reduction below standard equilibrium weight decreases the number of mature spawners. The effect of the linear sexual maturity of Equation (24) on the total population egg production is shown in Figure 5.

Figure 6 illustrates the response of a single P11000 trophic web with sexual maturity of species A modeled in this way. For the first 4 yr of the simulation run, input production at the food base level was about 20% of the standard equilibrium value; subsequently it was always at the standard equilibrium value. The reduced food supply resulted in stunting the population so much that from year 6 through 9 there was no recruitment. The subsequent reduced total food consumption by the greatly reduced population tended to bring the system into balance. If it survived, it would eventually return to standard equilibrium conditions. However, for this species with a lifespan of 6 yr or less, an interruption of recruitment for 4 yr is very dangerous. This, combined with a minimum population of about 1.4% of the standard at one point in the simulation, suggests that the condition reached here was very near a critical one for survival of the local species population. This

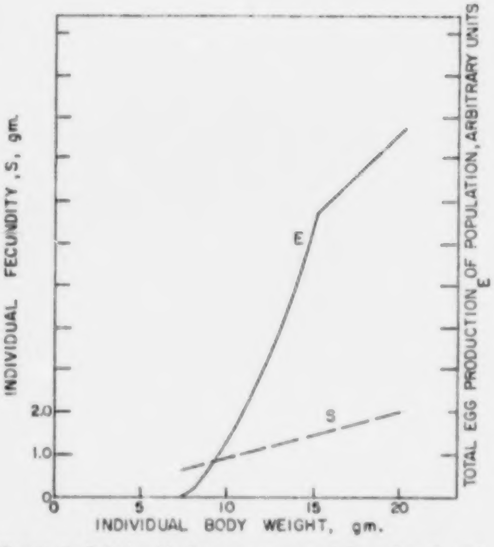

FIGURE 5.–Relationship between individual fecundity, S, and body weight and between total population egg production, E, and body weight. Sexual maturity is a linear function of body weight.

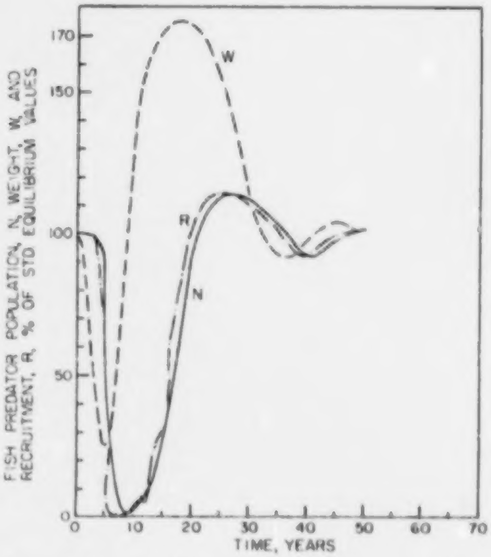

FIGURE 6.–Response of a single species, with sexual maturity a linear function of weight, to an initial 4-yr perturbation of low production by its prey. (P_1 = 20% of standard equilibrium value for the first four years.) Reproduction ceased between years 6 and 9. N = predator population; W = predator body weight; R = predator recruitment.

approach seems to offer a means of predicting the limits of stability of trophic webs against perturbation.

(B) Reproductive Time Lag

A limited study of the effects of the length of reproductive time lag was made using a representative individual model of the simplest trophic web, P11000 (a food base and the fish predator, species E). The food base was of the exponential growth type and the predator employed an Ivlev feeding function. Reproductive lags of 0, 2.50, and 6.25 yr were tried with a model that was otherwise basically the same. These three alternatives correspond respectively to the assumptions: 1) that offspring are mature when spawned, 2) that they take 2.50 yr to reach the "representative" stage, 3) that they take 6.25 yr to reach this stage. The second assumption is reasonable for species E.

The system was initially perturbed by starting with species E at 20% above its standard equilibrium population. The results for the biomass of species E are shown in Figure 7. It is clear that with increasing reproductive lag, the regulation of the system about its standard equilibrium becomes weaker; i.e., the biomass of species E, and other variables (not shown), reach more extreme oscillatory amplitudes. Larger amplitudes always incur greater risk of disaster. For example, in the runs shown here, a different sexual maturity criterion was used–knife-edge maturity at 80% of the standard equilibrium body weight. In the 6.25-yr lag run, this weight was reached at about 59 yr into the simulation, and after the 6.25-yr lag, it so reduced recruitment and the species E population that the system became unstable. This instability, which did not occur in the other runs, was due to the long lag in recruitment response to change in fecundity with changing food availability.

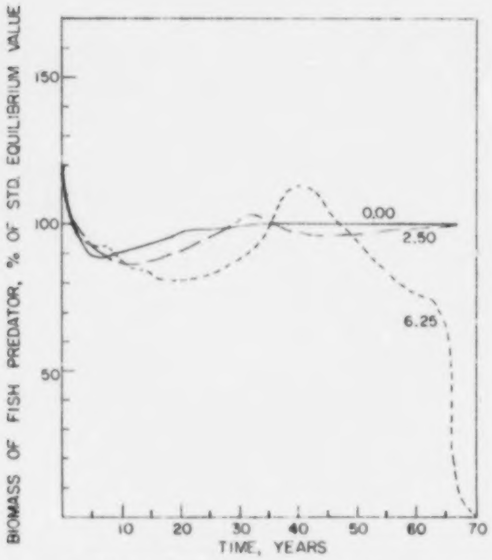

FIGURE 7.–Effects of reproductive time lag on the response of a single species to an initial perturbation in its population. The three cases illustrated have reproductive time lags of 0.00, 2.50, and 6.25 yr, respectively.

Except where otherwise stated, all the results presented here are for representative individual models having 2.50-yr lag and age class models having 2.00-yr lag. These are reasonable for the species involved. They are mutually consistent because in the age class model, reproductive products are summed over a full year and produce recruits 2.00 yr after the end of the year. Thus the average lag is about 2½ yr for the age class model also.

(C) Age Class Effects

A number of simulations were run with an explicit 4-age class model. Some results involving starvation have been shown above. Other exercises investigated the capabilities of this more accurate type of population model to regulate in the normal manner. Figure 8 illustrates the response of a simple food base-fish predator P11000 system with Ivlev feeding function to an initial perturbation of the fish predator population. The "mean total population" is a variable obtained by summing the populations of all the age classes, $\sum_{i=1}^{4} N_i$, during each computational increment of the year and taking the arithmetic average of these values. "Population mean annual biomass" is obtained by similarly summing and averaging the biomass values, $\sum_{i=1}^{4} N_i W_i$. These variables are shown in Figure 8 as percents of their standard equilibrium

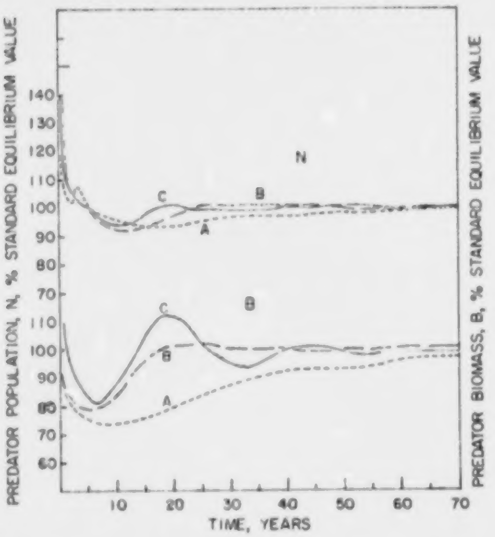

FIGURE 8.-Effects of age class structure and condition of recruits on the response of a single species to an initial overpopulation. (Curve A - 4-age class model with recruitment at standard recruit weight; curve B - 4-age class model with K_1 recruitment; curve C - representative individual model.) The three upper curves represent total species population, N; the three lower curves represent total species biomass, B.

values. In curve A, the system was represented by an explicit 4-age class model in which recruitment occurred at "standard recruit weight" (standard equilibrium weight for recruitment age). In curve B the model was identical except that recruitment occurred at K_1 times "standard recruit weight." The coefficient, K_1, is the ratio of the weight of the class ending its first recruited year to its standard equilibrium weight. Its use makes recruitment weight more consistent with current conditions. In curve C the system was represented by the corresponding representative individual model. Because of the way weight at recruitment is expressed, curves B and C are most directly comparable.

It is clear that there are some real differences in dynamics among all three models. These simulations and others indicate that for some detailed studies of the dynamics of trophic systems, age class models can provide additional information not available through representative individual models. However, much of the information of basic interest is contained in the representative individual solution. The final stable state is predicted accurately. Because of its lower damping, this model gives a conservative (maximum) estimate of the time required for the system to return to within any given range of this state, and this maximum is close enough to the actual time to be useful. For most variables and most perturbations, the maximum amplitudes of the age class model tend to be less than those of the representative individual model, so that the latter tends to predict an envelope of reasonable size within which the actual values will lie. These characteristics make the representative individual model especially useful for predicting stability.

The results shown and others suggest that the representative individual model can be used to approximate the behavior of the much more difficult and expensive age class model sufficiently well to justify use of the simpler model for many purposes. However, the quality of the approximation depends upon the characteristics of the particular system to be simulated. Where species are included that display a large range of sizes and ecological differences among the age classes of the recruited population, the representative individual approximation is likely to be less acceptable.

(D) Competition and Predation in More Complex Webs

A major purpose of the model developed here is to serve as a tool for study of more complex trophic systems. A few examples of particular interest are presented below.

In Figure 9 the trophic chain is extended by one link in the simplest possible manner to make a P11100 web. Species C preys on species A which preys on a constant input food base. Both interactions employ Holling feeding functions. The populations of all three trophic levels oscillated as the system returned from the initial perturbation of low food base biomass. Within about 3½ to 4 cycles (≈35 to 40 yr), all variables were within about 1% of standard equilibrium values again. The phase sequence of population and biomass rapidly became level 1, level 2, level 3 as would be expected. The population phase displacement was complicated by the 2½-yr reproductive lags and the effect of predation on the species A population (as species A lost weight, species C ate more species A individuals to meet its energy demands).

Such an extremely simple trophic web would be

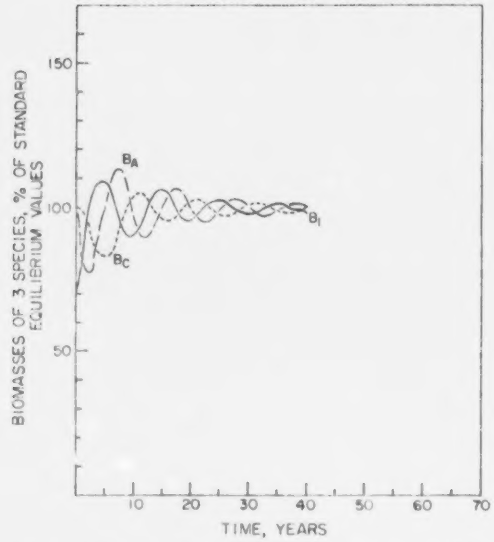

FIGURE 9.–Response of a simple 3-level trophic web (P11100) to an initial low prey abundance. (——— food base; ·········· 2nd level fish species; ----3rd level fish species.)

rare indeed in nature, but it is interesting for at least two reasons. The various species might be thought of as representing in some sense whole trophic levels of more extensive natural systems, each level consisting of a rather homogeneous group of species. If all the species at a single level have identical trophic parameters, this simple web in fact represents them exactly. This follows logically and has also been verified in simulation. Thus, the P11100 web model provides a base line for comparison for later unequal competition runs in a 3-level system. It represents the behavior of any *n* equally competing species at a trophic level, each with a population of 1/*n*th the total population. The P11000 web model provides the same kind of base line for competition in 2-level systems.

Figure 10 illustrates the simplest web, P11110, with four trophic levels: the food base and three fully modeled fish species. It consists of the P11100 web with species D added as a top predator. Again, an initial perturbation of low food base biomass caused oscillation of trophic variables of all species. After about 8 to 9 cycles (≈70 yr), all were within a very few percent of standard equilibrium values again. The same population and biomass phase sequence appears. Predation by species D caused quicker response of the species C population, reducing the phase displacement between species A and species C. The large phase displacement now occurred between species C and species D. The basic period of oscillation was also shortened from about 10 yr to about 8 yr. In all the above cases, maximum oscillation amplitudes of variables were less than the initial perturbation, and they rapidly became substantially less.

Effects produced on the system by feeding competition between species were of particular interest in these studies. No attempt was made to formulate explicit (interference) competition. Implicit competition was studied by constructing models with two predator species utilizing a common prey species. The P11000 and P11100 models above represent exactly equal competition at the second level in 2- and 3-level webs respectively.

The abstraction of exactly equal competition is not likely nor very interesting ecologically. A simple type of unequal competition is modeled by replacing one of the two species A-type competitors with species B, which is identical except that it has the advantage that its α_{starv} and $\alpha_{\max}$ are 70% of the species A values. Thus it has lower metabolic requirements and grows more for a given food intake. Figure 11 illustrates a simulation of this

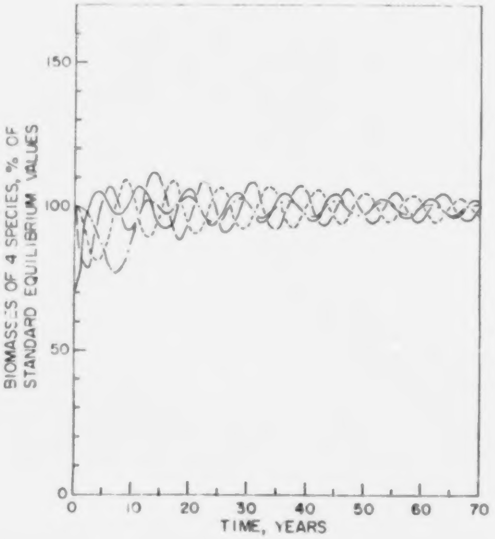

FIGURE 10.–Response of a simple 4-level trophic web (P11110) to an initial low prey abundance. (——— food base; ·········· 2nd level fish species; ----- 3rd level fish species; –·–·– 4th level fish species.)

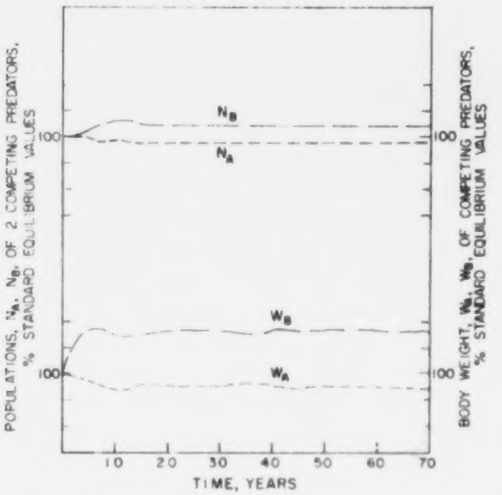

FIGURE 11.–Course of competition between two fish species with unequal metabolic demands, competing for a common food base. Species B is favored, since $\alpha_B = 0.7\,\alpha_A$. N_A = population of species A; N_B = population of species B; W_A = body weight of species A; W_B = body weight of species B.

2-level P12000 web started without initial perturbation, with identical body weights and populations of the two species. This situation is somewhat analogous to the simultaneous entry of the two competitors into an environment where the prey biomass and input are fairly close to the standard equilibrium values. The system moved away from the even start with oscillations which were firmly damped toward an apparent new steady state. In this state, the population and weight of the more capable competitor were increased relative to those of the less able contender. Their final relative positions might be characterized by the biomass ratio $B_B/B_A = 1.30$.

It is interesting to compare this prediction with that derived from the simpler graph theory analysis (Saila and Parrish 1972). This was accomplished by using the variable values from the present model for Q, B, and M to calculate the parameters q, h, a, b, and m for the graph theory model. These parameter values were then used in Equation (18) of Saila and Parrish (1972) to compute the biomass ratio $B_2/B_3 = 1.56$ of the competitors. This ratio is directly comparable with the ratio $B_B/B_A = 1.30$ from Figure 11. In view of the considerable differences in the two approaches, the agreement seems too good to be entirely fortuitous.

The above simulation represents simple unequal competition with the competitors' populations controlled by natural mortality and fecundity. Considerable theoretical and practical interest attaches to the influence of predatory mortality on such a system. Questions arise concerning whether more competing species can coexist, or whether competitors can coexist on a more even basis, where they are utilized by a common predator than in an otherwise similar environment without such top predation. Paine (1966) dealt with these questions by observation and field experiment and suggested that some intertidal systems seemed able to support more competing species when a top predator was present. Parrish and Saila (1970) explored a small number of cases by dynamic simulation of systems using Lotka-Volterra type interactions. Some competitive situations were found in which two unequally competing species persisted longer in more equal numbers when utilized by a top predator. Subsequently, May (1971) did a neighborhood stability analysis of the same systems and determined stability criteria in terms of competitive and predatory coefficients. Using coefficient values picked on this basis, Cramer and May (1972) used the Parrish and Saila model to demonstrate a case where an unstable two-species competition became stable when a common top predator was added to the system.

Figure 12 illustrates the behavior of a system with species C added as a top predator on the P12000 web of Figure 11. After some oscillation, the system moved to a new stable state with species C reduced to a level such that the competitors could support the total mortality. The stable relative biomasses of the competitors still reflect the competitive advantage of species B, but the ratio $B_B/B_A = 1.23$ is less than in the comparable 2-level system; i.e., the competitors occur in more nearly equal numbers. The result obtained by using the graph theory parameter values in Equation (19) of Saila and Parrish (1972) is $B_2/B_3 = 1.39$. When compared with the $B_2/B_3 = 1.56$ for the P12000 web, this also represents a more even standing among the competitors. Table 3 summarizes the B_B/B_A values obtained by dynamic simulation and by graph theory.

The same trend toward more equal biomasses of two species competing in the q coefficient when a common predator was present was found (Saila and Parrish 1972) using an independent set of "rough coefficients" provided by Menshutkin (1969). These comparisons of biomass ratios are

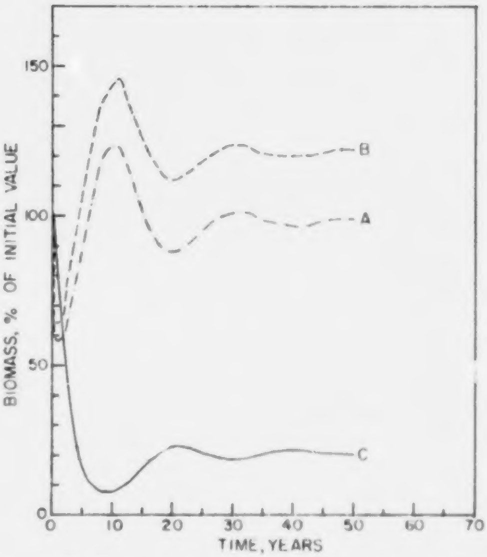

FIGURE 12.–Course of competition between two fish species, A and B, with unequal metabolic demands, competing for a common food base and utilized equally by a common predator, C. ($\alpha_B = 0.7\alpha_A$).

TABLE 3.–Biomass ratios for competing species.

Trophic system	Biomass of species with lower α / Biomass of species with higher α: Dynamic model prediction, B_B/B_A	Biomass of species with lower α / Biomass of species with higher α: Graph theory prediction, B_2/B_1
P12000 web	1.30	1.56
P12100 web	1.23	1.39

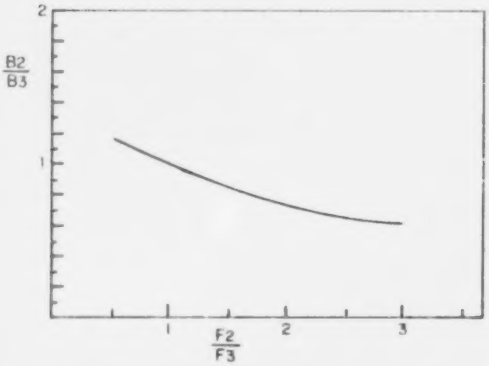

FIGURE 13.–Effect of differential exploitation on the biomass ratio, B_2/B_3, of two equally competing fish species: dynamic simulation prediction. The coefficient of instantaneous fishing mortality for species 3 is always $F_3 = 0.3$.

related to the concept of equitability diversity (Lloyd and Ghelardi 1964).

Some effects of human exploitation on systems of this kind have been briefly examined. Human exploitation on any species in any trophic web is expressed by the addition of Equation (18) to Equation (11) for that species (see MODEL section). Exploitation has been applied to two identical competitors in simple P12000 webs which were initially at standard equilibrium. It has produced the expected result of reducing both populations. Since the system is energy-controlled, there is always an accompanying increase in the competitors' body weights (which are always equal), and an increase in food base biomass, B_1. The total biomass of the competitor trophic level remains essentially constant. Differential exploitation of the two competitors affects the ratio of their numbers, and therefore also their biomass ratio. Figure 13 shows an example, using identical species A-type competitors that have arbitrarily been designated species 2 and species 3. This is the kind of curve produced by graph theory analysis for exploitation situations by Saila and Parrish (1972); e.g., their Figure 6, curve B. Parameter relationships are considerably different in the two papers. Natural mortality, M, in the present case is about 10 times its value in the Saila and Parrish paper. For another set of parameter values and a particular series of values of the exploitation coefficient, F, the stable B_2/B_3 ratio was predicted by both the dynamic simulation and the linear graph theory technique, as shown in Figure 14.

Exploitation of a comparable 3-level trophic web has also been simulated. A common predator, similar to species C except smaller, was added preying equally on two competitors almost identical with species A. A stable state for this unexploited system was found. Exploitation was applied to the competitors at various F values that had been used previously with the P12000 web. At sufficiently low values of F (in the range of Figure 14), in the new exploited steady state, the food base biomass, B_1, increased with exploitation of the competitors. The competitor with the lower F value increased in absolute population and biomass, while the more heavily exploited competitor decreased in both. Again, total biomass at the second trophic level remained essentially constant. In all cases, population and body weight of the predator decreased markedly when the competi-

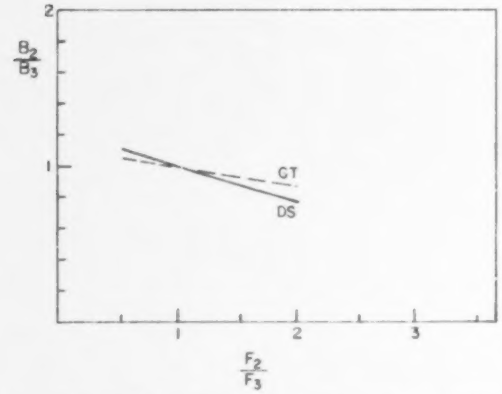

FIGURE 14.–Effect of differential exploitation on the biomass ratio, B_2/B_3, of two equally competing fish species: predictions of dynamic simulation (DS) and graph theory (GT). The coefficient of instantaneous fishing mortality for species 3 is always $F_3 = 0.1$.

tors were exploited. The ratio B_2/B_3 from the simulation at a given F_2/F_3 ratio was slightly less extreme than in the P12000 web. However, the difference was too slight to permit a meaningful check against graph theory calculations.

The top predator in this system could also be exploited using low values of F. The results were qualitatively similar to the last case above. The B_2/B_3 ratio changed only very slightly in this particular system to values intermediate between those of the last case above and those obtained with the P12000 web. At even the lowest F values for the competitors in Figure 14, if exploitation of the top predator was carried above about $F = 0.2$, the top predator was lost from the system. The same result occurred with $F \leq 0.2$ on the top predator if slightly higher F values than those in Figure 14 were applied to the competitors. The two lower trophic levels persisted stably. This vulnerability of the top predator represents another limit to the stability of the larger system. Although it has not been explored, it appears to have implications for possible effects of exploiting real multispecies fisheries.

The particular combinations used in this brief investigation were far from optimum for exploring a large range of exploitation intensities in multilevel webs (The choices were made primarily for similarity to other cases studied previously). The low permissible levels of predation and exploitation that the 3-level system would tolerate, together with the high natural mortality, made for difficulty in comparing results with those of trophic systems previously examined; e.g., by graph theory. However, the considerable similarity of the predictions in Figure 14 and Table 3 by these very different approaches seems highly suggestive.

AVAILABILITY OF MODEL AND COMPUTING DETAILS

Written descriptions of various portions of the model and their sources in somewhat more detail are available from the author. The basic computer software package used (IBM 1969) and a more advanced version (IBM 1971) are described in the manufacturer's literature with enough detail in the former case for ready use by the reader. The CSMP package is sufficiently user-oriented that no further interface program is required; the model is written directly into the CSMP structure using simplified FORTRAN-like statements. Program listings and card decks for sample trophic models are available from the author, together with tables of input values used and a glossary of code names of variables and parameters.

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LITERATURE CITED

ADELMAN, H. M., J. L. BINGHAM, AND J. L. MAATCH.
1955. The effect of starvation upon brook trout of three sizes. Prog. Fish-Cult. 17:110-112.
BAGENAL, T. B.
1957. The breeding and fecundity of the long rough dab *Hippoglossoides platessoides* (Fabr.) and the associated cycle in condition. J. Mar. Biol. Assoc. U.K. 36:339-375.
1967. A short review of fish fecundity. *In* S. D. Gerking

(editor), The biological basis of freshwater fish production, p. 89-111. Blackwell, Oxf. and Edinb.

Bagenal, T. B., and E. Braum.

1971. Eggs and early life history. *In* W. E. Ricker (editor), Methods of assessment of fish production in fresh waters, p. 166-198. Blackwell, Oxf. and Edinb.

Beamish, F. W. H., and L. M. Dickie.

1967. Metabolism and biological production in fish. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 215-242. Blackwell, Oxf. and Edinb.

Beverton, R. J. H.

1962. Long-term dynamics of certain North Sea fish populations. *In* E. D. LeCren and M. W. Holdgate (editors), The exploitation of natural animal populations, p. 242-259. Blackwell Sci. Publ. Ltd., Oxf.

Beverton, R. J. H., and S. J. Holt.

1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish Food (G.B.), Ser. II, 19, 533 p.

1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Found. Colloq. Ageing 5:142-180.

Bigelow, H. B., and W. C. Schroeder.

1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

Box, G. E. P.

1954. The exploration and exploitation of response surfaces: Some general considerations and examples. Biometrics 10:16-60.

Box, G. E. P., L. R. Connor, W. R. Cousins, O. L. Davies, F. R. Himsworth, and G. P. Sillitto.

1953. The design and analysis of industrial experiments. O. L. Davies (editor), Oliver and Boyd, Edinb.

Box, G. E. P., and J. S. Hunter.

1957. Multi-factor experimental designs for exploring response surfaces. Ann. Math. Stat. 28:195-241.

Brett, J. R.

1962. Some considerations in the study of respiratory metabolism in fish, particularly salmon. J. Fish. Res. Board Can. 19:1025-1038.

Brett, J. R., J. E. Shelbourn, and C. T. Shoop.

1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhyncus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363-2394.

Cramer, N. F., and R. M. May.

1972. Interspecific competition, predation and species diversity: a comment. J. Theor. Biol. 34:289-293.

Davis, C. C.

1968. Quantitative feeding and weight changes in *Poecilia reticulata*. Trans. Am. Fish. Soc. 97:22-27.

Davis, G. E., and C. E. Warren.

1965. Trophic relations of a sculpin in laboratory stream communities. J. Wildl. Manage. 29:846-871.

1971. Estimation of food consumption rates. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 204-225. Blackwell, Oxf. and Edinb.

Dawes, B.

1930. Growth and maintenance in the plaice (*Pleuronectes platessa* L.). Part I. J. Mar. Biol. Assoc. U.K. 17:103-174.

Holling, C. S.

1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91:385-398.

International Business Machines Corporation.

1969. System/360 continuous system modeling program (360A - CX - 16X) user's manual H20-0367-3.

1971. Program product continuous system modeling program (CSMP III) and graphic feature (CSMP III graphic feature) general information manual. Program no. 5734-XS9.

Ivlev, V. S.

1961a. [On the utilization of food by plankton-eating fishes.] Tr. Sevastopol'. Biol. Stn. 14:188-201. (Transl. 1963, Fish. Res. Board Can. Transl. Ser. 447.)

1961b. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, 302 p.

Karpov, V. G., F. V. Krogius, I. M. Krokhin, and V. V. Menshutkin.

1969. [Model of the ichthyocoenosis in Dalnee Lake realized on an electronic computer.] Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 67:76-87. (Transl. 1970, Fish Res. Board Can. Transl. Ser. 1572.)

Kausch, H.

1968. [The effect of spontaneous activity on the metabolic rate of young carp (*Cyprinus carpio* L.) when starving and fed.] Arch. Hydrobiol./Suppl. 33 (3/4):263-330.

Kostitzin, V. A.

1939. Mathematical biology. George G. Harrap & Co. Ltd., Lond., 238 p.

Krogius, F. V., E. M. Krokhin, and V. V. Menshutkin.

1969. [The pelagic fish community in Lake Dalnee. An experiment in cybernetic modelling.] Akad. Nauk SSSR, KOTINRO Inst. Evol. Fiziol. Biol. I. M. Sechenov AN SSSR. Leningrad, "Nauka," p. 1-86. (Transl. 1970, Fish Res. Board Can. Transl. Ser. 1486.)

Lassiter, R. R., and D. W. Hayne.

1971. A finite difference model for simulation of dynamic processes in ecosystems. *In* B. C. Patten (editor), Systems analysis and simulation in ecology, 1:367-440. Academic Press, N.Y.

Lawrencz, W. M.

1940. The effect of temperature on the weight of fasting rainbow trout fingerlings. Trans. Am. Fish Soc. 70:291-296.

LeCren, E. D.

1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years with special reference to the effects of temperature and changes in population density. J. Anim. Ecol. 27:287-334.

1962. The efficiency of reproduction and recruitment in freshwater fish. *In* E. D. LeCren and M. W. Holdgate (editors), The exploitation of natural animal populations, p. 283-302. Blackwell, Oxford.

1965. Some factors regulating the size of populations of freshwater Fish. Mitt. Int. Ver. Theor. Angew. Limnol. 13:88-105.

Lloyd, M., and R. J. Ghelardi.

1964. A table for calculating the 'equitability' component of species diversity. J. Anim. Ecol. 33:217-225.

Mackay, I., and K. H. Mann.

1969. Fecundity of two cyprinid fishes in the River Thames, Reading, England. J. Fish. Res. Board Can. 26:2795-2805.

Mann, K. H.

1965. Energy transformations by a population of fish in the river Thames. J. Anim. Ecol. 34:253-275.

1967. The cropping of the food supply. *In* S. D. Gerking

(editor), The biological basis of freshwater fish production, p. 243-257. John Wiley & Sons, N.Y.
1969. The dynamics of aquatic ecosystems. Adv. Ecol. Res. 6:1-81.
May, R. M.
1971. Stability in multispecies community models. Math. Biosci. 12:59-79.
Menshutkin, V. V.
1968. [Fish populations competition for food analyzed.] Zool. Zh. 47:1597-1602. (Transl. Natl. Tech. Inf. Serv., Springfield, Va., JPRS 47, 345.)
1969. [Graph theory applied to aquatic organism communities.] Zh. Obshch. Biol. 1969(1):42-49. (Transl. Natl. Tech. Inf. Serv., Springfield, Va., JPRS 47,689.)
Menshutkin, V. V., and Y. Y. Kislyakov.
1967. [Simulation of a population of a commercial fish assuming a variable growth rate.] Zool. Zh. 46:805-810. (Transl. Div. Fish. Res., U.S. Bur. Sport Fish., Wildl.).
1968. [Simulation of the influence of the food supply on the dynamics of a fish population.] Zool. Zh. 47:341-346. (Transl. Div. Fish. Res., U.S. Bur. Sport Fish. Wildl.).
Menshutkin, V. V., and T. I. Prikhodko.
1968. [Investigation of production process on models of the simplest populations of water animals.] Gidrobiol. Zh. 4:3-11. (Transl. Off. Foreign Fish., Natl. Mar. Fish. Serv.)
1969. Productive properties of stable populations with a prolonged period of reproduction. Hydrobiol. J. 5(1):1-7.
1970. Simulation of the population of planktonic crustaceans by electronic computer. Oceanol. Acad. Sci. USSR 10:261-265.
Menshutkin, V. V., and A. A. Umnov.
1970. A mathematical model of a very simple aquatic ecosystem. Hydrobiol. J. 6(2):18-23.
Nikolskii, G. V.
1961. [Concerning the cause of fluctuations in the abundance of fishes.] Vopr. Ikhtiol. 1:659-665. (Transl. 1962, Fish. Res. Board Can. Transl. Ser. 389.)
1962. On some adaptations to the regulation of population density in fish species with different types of stock structure. *In* E. D. LeCren and M. W. Holdgate (editors), The exploitation of natural animal populations, p. 265-282. Blackwell, Oxford.
Norden, C. R.
1967. Age, growth and fecundity of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Trans. Am. Fish. Soc. 96:387-393.
Paine, R. T.
1966. Food web complexity and species diversity. Am. Nat. 100:65-77.
Paloheimo, J. E., and L. M. Dickie.
1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Board Can. 22:521-542.
1966. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Board Can. 23:869-908.
Parrish, J. D., and S. B. Saila.
1970. Interspecific competition, predation and species diversity. J. Theor. Biol. 27:207-220.
Phillips, A. M., Jr.
1954. Effect of starvation upon brook and rainbow trout. Prog. Fish-Cult. 16:124.
1969. Nutrition, digestion, and energy utilization. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, 1:391-432. Academic Press, N.Y.
Pitt, T. K.
1964. Fecundity of the American plaice, *Hippoglossoides platessoides* (Fabr.) from Grand Bank and Newfoundland areas. J. Fish. Res. Board Can. 21:597-612.
Saila, S. B., and J. D. Parrish.
1972. Exploitation effects upon interspecific relationships in marine ecosystems. Fish. Bull., U.S. 70:383-393.
Scott, D. P.
1962. Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. J. Fish Res. Board Can. 19:715-731.
Simpson, A. C.
1951. The fecundity of the plaice. Fish. Invest. Minist. Agric. Fish Food (G.B.), Ser. II, 17(5):1-27.
Ten, V. S.
1967. [Trophic interactions of simple predator-prey pairs among aquatic organisms.] Respubl. Mezhvedomstvennyi Sbornik, Ser. "Biol. Morya" Akad. Nauk Ukrain. SSR "Naukova Dumka" Kiev, Pap. 2:16-43. (Fish. Res. Board Can. Transl. Ser. 972.)
Ursin, E.
1967. A mathematical model of some aspects of fish growth, respiration and mortality. J. Fish. Res. Board Can. 24:2355-2453.
Warren, C. E., and G. E. Davis.
1967. Laboratory studies on the feeding, bioenergetics and growth of fish. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 175-214. Blackwell, Oxf. and Edinb.
Winberg, G. G.
1956. [Rate of metabolism and food requirements of fish.] Nauchnye Tr. belorussk. Gos. Univ., Minsk., 253 p. (Transl. 1960, Fish. Res. Board Can. Transl. Ser. 194.)
1962. [The energy principle in studying food associations and the productivity of ecological systems.] Zool. Zh. 41:1618-1630. (Fish. Res. Board Can. Transl. Ser. 433.)
Woodhead, A. O.
1960. Nutrition and reproductive capacity in fish. Proc. Nutr. Soc. 19:23-28.

APPENDIX

The parameter, s, in the starvation mortality Equations (16) and (17) is found as follows:

During starvation, since $kC < Q$ and $S = 0$, Equation (1) simplifies to

$$G = \frac{dW}{dt} = kC - Q = kC - \alpha W^{\gamma} \qquad \text{(A-1)}$$

At any constant level of ration, C, this integrates to give

$$t = \frac{5j}{4\alpha}\left[\ln\left|\frac{j + W^{0.20}}{j - W^{0.20}}\right| + 2\tan^{-1}\frac{W^{0.20}}{j}\right] - \frac{5W^{0.20}}{\alpha} - I_1. \qquad \text{(A-2)}$$

where: $j = \left(\frac{kC}{\alpha}\right)^{0.25}$.

I_1 is a constant of integration. Taking the boundary condition that $W = W_0$; i.e., the initial weight of each original N_0 individual, at time $t = 0$, the constant I_1 can be evaluated any any level of ration.

The boundary condition at 100% mortality is taken to correspond with a critical fraction–0.6–of the body weight of a normal, well-fed individual (the critical fraction is estimated from a variety of sources, including: Dawes 1930; Lawrence 1940; Phillips 1954; Adelman et al. 1955; Brett 1962; Brett et al. 1969). Using this critical lethal body weight for W, Equation (A-2) can be solved to give the critical time, t_c, to 100% mortality. Using this t_c in Equation (16) when $N/N_0 = 0$ gives the value of s.

HOMING BEHAVIOR AND CONTRIBUTION TO COLUMBIA RIVER FISHERIES OF MARKED COHO SALMON RELEASED AT TWO LOCATIONS

Robert R. Vreeland,[1] Roy J. Wahle,[1] and Arthur H. Arp[2]

ABSTRACT

This study was initiated to determine the feasibility of creating or enhancing fisheries in specific areas by releasing salmon smolts into those areas. In 1970, two groups each of approximately 100,000 1968-brood coho salmon, *Oncorhynchus kisutch*, were marked with a right ventral (RV) or a left ventral (LV) finclip at Little White Salmon National Fish Hatchery near Cooks, Wash. The LV-marked group was transported by truck to Youngs Bay, 19 km (12 miles) from the mouth of the Columbia River near Astoria, Oreg., and released in April 1970. The RV-marked group was released in May 1970 at Little White Salmon Hatchery, 242 km (150 miles) from the mouth of the Columbia River. The Youngs Bay and Columbia River gill-net fisheries were sampled for these marks in the fall of 1970 and 1971. The two groups homed to their respective areas of release with very little straying. The LV-marked group contributed 7.7 fish to the fisheries sampled for each 1,000 fish released, and the RV-marked group contributed 11.7 fish to the fisheries sampled per 1,000 fish released. However, a fair comparison of the contribution of the two groups is inhibited by 1) incomplete sampling for these marks in the ocean fisheries, 2) the difference in time and size of release of the groups, 3) the unknown effect of delayed mortality due to hauling the LV-marked group, and 4) duplication of these marks in the ocean fisheries.

The Pacific salmon, *Oncorhynchus* spp., hatchery program has undergone considerable evolution in the past 10 yr. The escapement of adult fish to hatcheries is often more than sufficient to supply egg needs. In many cases, hatcheries receive sizable excesses of returning adults. These fish must be disposed of either by releases into streams, burial, donations, or sales. The sale of salmon carcasses has caused considerable friction between commercial fishermen and fishery agencies. Salmon returning to hatcheries often arrive in a condition which makes them unsuitable for donation or release into streams. Burial of the excess salmon is an obvious waste of a valuable resource.

Taft and Shapovalov (1938) found the homing instinct of coho salmon, *O. kisutch*, to the parent stream to be fairly exact. Hasler and Wisby (1951), Wisby and Hasler (1954), and Groves et al. (1968) reported the importance of olfaction in homing of adult salmon. Hasler (1966) and Wagner (1969) felt that the organic odor of the parent stream was imprinted rapidly in juvenile salmon, possibly at the time of downstream migration. We felt that if the homing instinct was exact and the homestream imprint was acquired quickly during parr-smolt transformation, then the homing site could be altered by transportation and release of coho salmon smolts.

The purpose of this study was to determine the feasibility of creating or enhancing fisheries in specific areas by releasing salmon smolts in those areas. If salmon returned to the area of release, the problem of excess hatchery returns could be reduced. This homing behavior would provide local fisheries with larger catches of salmon and a longer fishing season.

Youngs Bay was the site picked for testing the homing behavior of salmon. It is about 19 km (12 miles) upstream from the mouth of the Columbia River near Astoria, Oreg. The Lewis and Clark, Walluski, Youngs, and Klaskanine rivers empty into Youngs Bay (Figure 1). All are small rivers with low summer flows and greatly fluctuating winter flows. The Klaskanine Salmon Hatchery, operated by the Fish Commission of Oregon, is located on the North Fork of the Klaskanine River (Weiss 1966).

A commercial salmon fishery began on Youngs Bay in the early 1900's. The bay was closed to commercial fishing from 1931 to 1962, but has remained open from 1962 to present. From 1962 to

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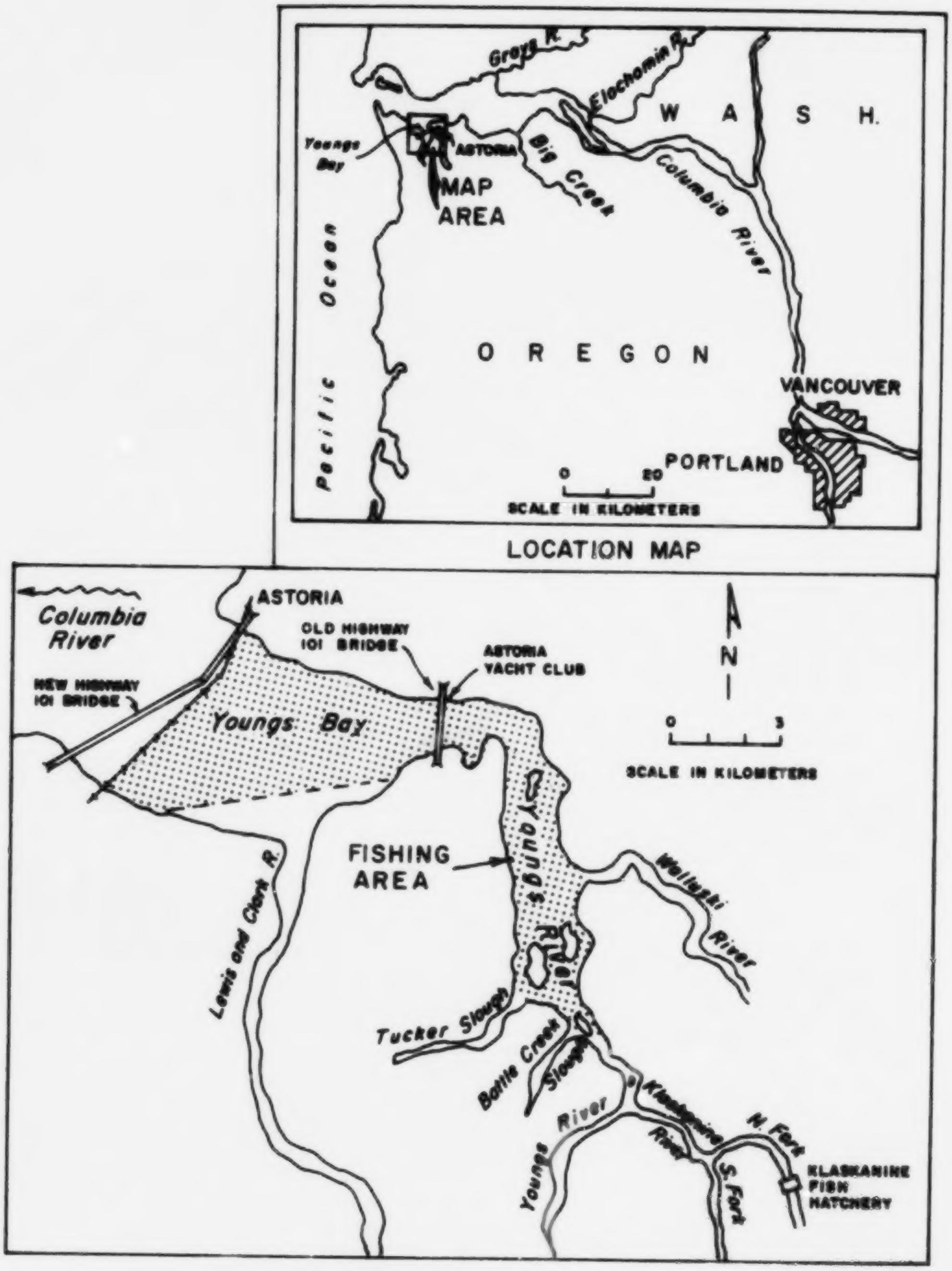
Grays R.
Elochoman R.
W A S H.
Youngs Bay
ASTORIA
Big Creek
Columbia River
MAP AREA
Pacific Ocean
O R E G O N
VANCOUVER
PORTLAND
0
20
SCALE IN KILOMETERS
LOCATION MAP
Columbia River
ASTORIA
OLD HIGHWAY 101 BRIDGE
ASTORIA YACHT CLUB
NEW HIGHWAY 101 BRIDGE
Youngs Bay
N
0
3
SCALE IN KILOMETERS
FISHING AREA
Youngs River
Wallooskee River
Lewis and Clark R.
Tucker Slough
Battle Creek Slough
Klaskanine River
N. Fork
S. Fork
Youngs River
KLASKANINE FISH HATCHERY

FIGURE 1.–Youngs Bay, Oreg.

1965, the fishing area extended from Battle Creek slough to the old Highway 101 bridge (Figure 1). The open area was extended to the new Highway 101 bridge in 1965. Coho salmon is the main species caught, but some chum salmon, *O. keta*, chinook salmon, *O. tshawytscha*, and steelhead trout, *Salmo gairdneri*, are also taken (Weiss 1966). The coho fishery has fluctuated from a low of 2,100 adults in 1962 to a high of 31,600 adults in 1967.[1]

The sport fishery in Youngs Bay itself is very limited. A majority of the sport fishing occurs from the confluence of the North and South forks of the Klaskanine River upstream to the Klaskanine Salmon Hatchery. A minor sport fishery for coho salmon exists on the Youngs River. It is limited by an impassable falls a short distance upstream from the river's confluence with Youngs Bay. There is little or no sport fishing for salmon on the Lewis and Clark or Walluski rivers. Sport fishing for coho in Youngs Bay and its tributaries starts after the first fall rains, from mid-September to the first of October.[2]

METHODS AND MATERIALS

Source of Fish

Coho salmon were selected as the test species for this study because of the success of hatchery coho culture exhibited by large hatchery returns. The coho for this experiment were obtained from Little White Salmon National Fish Hatchery. The eggs were taken in 1968 at Klaskanine Salmon Hatchery, and 926,300 were shipped to Little White Salmon Hatchery for hatching and rearing. Eggs from coho returning to Little White Salmon Hatchery were not reared at the station because the stock was considered undesirable. This stock had inadvertently been selected to commingle with the hatcheries fall chinook returns. This made it difficult to retain coho in good condition until spawning time. The Klaskanine coho were a later returning stock and would presumably eliminate the conflict with fall chinook.

Little White Salmon Hatchery is located near Cooks, Wash. on the Little White Salmon River approximately 1.5 km (1 mile) upstream from its confluence with the Columbia River and is about 242 km (150 river miles) from the Pacific Ocean. The hatchery is operated by the U.S. Fish and Wildlife Service and is funded primarily by the National Marine Fisheries Service.

Marking

The marking portion of the study took place in March 1970. A total of 201,700 1968-brood coho salmon were marked with a finclip at Little White Salmon Hatchery. The right ventral (RV) fin was removed from 100,809 coho which were to be released in the Little White Salmon River. The left ventral (LV) fin was removed from 100,914 fish which were to be released into Youngs Bay. Fish were 55-62/kg (25-28/pound) at time of marking.

Release Procedures

Youngs Bay was selected as a release site for three reasons. First, the bay is within the Columbia River system and yet a great enough distance from the Little White Salmon Hatchery to examine homing characteristics of coho salmon. Second, the bay provides a specific area separate from the Columbia River to which the salmon could home. Finally, the intensive commercial fishery in the bay was somewhat separate from the Columbia River fishery and would be relatively easy to sample.

A total of 100,662 LV-marked coho salmon weighing 2,019 kg (4,451 pounds) or 49.8 fish/kg (22.6/pound) were transported from the Little White Salmon Hatchery to Youngs Bay on 23, 27, and 29 April 1970. This was the normal historical coho release time at the hatchery. Two hatchery tank trucks, each making one trip per day, were used to transport the fish. On the first trip the water in the trucks was iced to maintain a constant temperature during transportation. The weather was rainy and cold, and the result was 2°C lower water temperature in the trucks than in the bay. Bay water was added to the tanks to equalize the two temperatures. The weather was the same on ensuing trips so icing was discontinued. The dates and water temperatures at the time of release are as follows:

		Temperature (°C)	
Date	*Time*	*Bay*	*Truck*
23 April	1930	11.1	10.6
27 April	2000	10.0	10.6
30 April	2000	11.1	10.6

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[1] James L. Galbreath. 1968. Youngs Bay commercial coho fishery in 1967. Fish Comm. Oreg., Fish Comm. Res. Lab., Clackamas, Oreg. (Unpubl. manuscr., 10 p.)

[2] Franklin R. Young. Fish Comm. Manage. Res. Hdqrs., Clackamas, Oreg. (Pers. commun.).

The Astoria Yacht Club boat launching ramp (Figure 1) was chosen as the release site in Youngs Bay. It provided easy access and no spawning gravel or stream mouths occurred near the site. We hoped that returning adult coho salmon would mill around the bay in search of a stream. This would provide ample opportunity for commercial fishermen to harvest the fish.

All releases were made at dusk to reduce predation by gulls, grebes, ducks, and resident fish. The smolts dispersed rapidly upon release, most of them swimming toward deeper water. Movements could be seen as far as 100 m from shore shortly after releases. Only one instance of predation by birds was observed, and initial transportation losses were negligible. All the fish appeared health and active upon release.

The RV-marked coho salmon were released directly from the Little White Salmon Hatchery rearing ponds into the Little White Salmon River on the evening of 12 May 1970. A total of 100,367 fish weighing 2,504 kg (5,520 pounds) or 40.1 fish/kg (18.2/pound) were liberated. The RV-marked group was released 2 wk later than the Youngs Bay group. The reason for this difference in release dates is unknown.

Sampling

In the fall of 1970, we sampled the Youngs Bay commercial fishery for marked 2-yr-old coho salmon. The sampling was concentrated at The New England Fish Company. A fish buyer, Lawrence Peterson, was contracted by New England Fish Company to purchase fish from Youngs Bay commercial fishermen and deliver them to the processing plant. We also did some sampling of the Youngs and Klaskanine rivers sport fisheries. The Columbia River commercial fishery was sampled by the Fish Commission of Oregon. The California ocean fisheries were not sampled for single fin marks and the British Columbia and Alaska ocean fisheries and Columbia River sport fisheries were not sampled for marked fish.

Returns to hatcheries near Youngs Bay were examined for stray LV- or RV-marked coho salmon. The major effort was concentrated at the Klaskanine Salmon Hatchery since it is the only hatchery on a tributary of Youngs Bay. Returns to Big Creek Salmon Hatchery on Big Creek near Knappa, Oreg., the Elokomin Salmon Hatchery on the Elochomin River near Cathlamet, Wash., and the Grays River Salmon Hatchery on the Grays River near Grays River, Wash., were examined for LV- and RV-marked coho (Figure 1). The coho returning to Little White Salmon National Fish Hatchery were also checked for marks.

The sampling in the fall of 1971 was similar to that done in 1970. The only differences being that the sampling effort was concentrated at Barbey Packing Corporation in Astoria, and there was no sampling of the Youngs and Klaskanine River sport fisheries.

RESULTS

1970 Sampling Season

The Youngs Bay gill-net season began on 13 September 1970 and ended on 31 October 1970, a total season of 49 days. Sampling for marked 1968-brood coho jack salmon at the New England Fish Company took place on 13 of the 49 days (jack salmon are predominately males that mature early and that on the average are considerably smaller than the normal adult fish). The entire catch of coho jacks was examined on the days sampled. The total catch of jacks was estimated at 2,300 in the Youngs Bay fishery in 1970.[1] Of these, 952 were examined for marks for a 41.4% sample. Only two LV-marked and no RV-marked coho were found. This is to be expected since most fishermen use nets of 15.9-cm (6¼-inch) stretched mesh size for adult coho because of the higher price paid for adults. Table 1 shows the days sampled, the total weight and number of coho examined by day, and the marks found.

The Klaskanine River sport fishery was sampled on 23, 24, 25, 26, and 30 September. No marks were found on 18 coho jacks examined.

The Fish Commission of Oregon sampled the Columbia River commercial fishery in 1970. Only two marked coho jacks were found, one LV and one RV. This was again due to the use of 15.9-cm or larger mesh size gill nets for adult chinook and coho.

There was no concentrated sampling effort for the LV- and RV-marked coho salmon in the Columbia River sport fishery or the California, British Columbia, or Alaska ocean commercial and sport fisheries. Also, duplication of these marks in the ocean fisheries precluded their assignment to specific experiments. Table 2 lists the number of

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[1] James L. Galbreath, Fish Comm. Manage. Res. Hdqrs., Clackamas, Oreg. (Pers. commun.).

TABLE 1.–Weight, number, and marks of 1968-brood coho salmon examined by sample day during the 1970 Youngs Bay gill-net season.[1]

Date 1970	Weight (kg)	Number	Marks			
			LV	Ad-LV	Ad-RV	Ad
9/17	—	14	—	1	—	—
18	—	7	—	—	—	—
22	147	125	—	—	—	—
23	82	77	—	—	—	—
24	147	126	1	—	—	—
25	186	137	—	—	—	—
26	106	90	—	—	—	—
27	87	70	—	—	—	—
28	—	68	—	—	—	—
30	104	118	1	—	1	—
10/ 6	—	12	—	—	—	—
7	69	58	—	—	—	1
8	—	50	—	—	—	—
Total	930	952	2	1	1	1

[1]The sampling was done at New England Fish Co. unloading dock.

1968-brood LV- and RV-marked coho recovered by year, area, and fishery.

The returns of Klaskanine, Big Creek, Grays River, Elokomin, and Little White Salmon hatcheries were examined for LV- and RV-marked 1968-brood coho salmon. A total of 9,039 jacks returned to Klaskanine Hatchery and 8,705 were examined for marks. Only three LV and no RV marks were observed. No LV or RV marks were found in the returns to the other three hatcheries. At Little White Salmon Hatchery, 1 LV-marked and 55 RV-marked coho were observed. Table 3 lists the number of marked 1968-brood coho returning to the five previously mentioned hatcheries by hatchery, year, and mark.

1971 Sampling Season

In 1971 the sampling for marks was done at Barbey Packing Corporation, Astoria, Oreg. The entire catch of coho salmon was examined on 27 days of the 49-day season. The catch of 1968-brood coho was estimated to be 8,110 fish. Of these, 5,477 were examined for marks for a 67.5% sample. Table 4 shows the days sampled, the weight and numbers of coho sampled, and the marks found. A total of 355 marked coho were observed, of which 336 were LV marked and 8 were RV marked (Table 4). Length and weight data were collected from 320 of the marked 1968-brood coho examined. These data are presented in Table 5.

The sport fisheries of Youngs Bay and its tributaries were not sampled in 1971, but the Fish Commission of Oregon again sampled the Columbia River gill-net fishery for marks. A total of 17 LV-marked and 74 RV-marked 1968-brood coho salmon were recovered. As in 1970, the Columbia River sport, California, British Columbia, and Alaska ocean sport, and ocean commercial fisheries were not sampled for LV- or RV-marked coho.

TABLE 2.–Number of 1968-brood LV- and RV-marked coho salmon recovered by year, area, and fishery, 1970 and 1971.[1]

Area and fishery	1970		1971	
	LV	RV	LV	RV
Youngs Bay gill net	2	0	336	8
Youngs Bay sport	0	0	—	—
Columbia River gill net	1	1	17	74
Total	3	1	353	82

[1]Columbia River and ocean sport and ocean commercial fisheries were not sampled for these marks.

TABLE 3.–Number of 1968-brood LV- and RV-marked coho salmon recovered at five Columbia River hatcheries by year, 1970 and 1971.

Hatchery	1970		1971	
	LV	RV	LV	RV
Klaskanine	3	0	1	0
Big Creek	0	0	1	0
Grays River	0	0	0	1
Elokomin	0	0	0	0
Little White Salmon	1	55	3	300
Total	4	55	5	301

Hatchery returns examined in 1970 were again examined in 1971. Klaskanine Hatchery had an adult coho return of 5,476 fish. Only one LV-marked and no RV-marked fish were found. No RV- or LV-marked adults were seen at Big Creek or Elokomin hatcheries, and only one RV mark was recovered at Grays River Hatchery. At Little White Salmon Hatchery, 300 RV-marked and only 3 LV-marked 1968-brood coho were recovered. (See Table 3.)

The estimated catches of marked 1968-brood coho salmon by fishery, year, and mark are presented in Table 6. These values were obtained by multiplying the total 1968-brood coho catch for a fishery by the rate of occurrence of a mark in that fishery. Columbia River gill-net estimates were calculated for weekly periods and summed for the season. The Youngs Bay marked fish estimates were made for the entire fall season. For example, it was estimated that 8,110 1968-brood coho were caught in Youngs Bay in 1971 (Table [illegible]). Of these fish 5,477 were sampled for marks and 336 LV marks were observed. Thus the estimated catch of LV marks was 8,110×336/5,477 = 498.

TABLE 4.–Weight, number, and marks of 1968-brood coho salmon caught each day during the 1971 Youngs Bay gill-net season.[1]

Date 1971	Weight (kg)	Number	Marks						
			LV	RV	Ad	Ad-LV	Ad-RV	Ad-LM	Ad-RM
9/17	1,007	236	—	—	—	—	—	—	—
18	1,204	282	—	—	—	—	—	—	—
19	1,427	334	—	—	—	—	—	—	—
20	929	217	—	—	—	—	—	—	—
21*	1,457	305	12	—	—	—	—	—	—
22*	1,132	260	12	—	—	—	—	—	—
23*	910	210	9	1	1	—	—	—	—
24	835	195	—	—	—	—	—	—	—
25*	1,064	240	14	—	—	—	—	—	—
26*	1,289	296	17	—	—	—	—	—	—
27*	434	96	4	—	—	—	—	—	—
28*	406	99	3	1	—	—	—	—	—
29	650	152	—	—	—	—	—	—	—
30*	978	225	6	—	—	—	—	—	—
10/ 1*	1,341	305	8	—	—	—	—	—	—
2*	1,135	265	14	—	—	—	—	—	—
3*	1,289	307	17	1	—	—	—	—	—
4*	552	128	7	—	—	—	—	—	—
5*	2,085	503	31	1	—	—	—	—	—
6*	1,084	271	18	—	—	1	—	—	—
7*	980	222	29	1	—	—	—	3	—
8*	627	144	14	1	—	—	2	—	1
9*	786	185	6	1	—	—	—	—	—
10*	725	173	12	—	1	—	1	—	—
11*	668	152	14	—	1	—	—	—	—
12*	583	137	5	—	—	—	—	—	—
13	477	112	—	—	—	—	—	—	—
14	901	211	—	—	—	—	—	—	—
15*	716	172	12	—	—	—	—	—	—
16*	615	147	8	—	—	—	—	—	—
17*	690	161	13	—	—	—	—	—	—
18	489	115	—	—	—	—	—	—	—
19	494	116	—	—	—	—	—	—	—
20	811	190	—	—	—	—	—	—	—
21	1,070	250	—	—	—	—	—	—	—
22*	786	186	18	1	—	—	—	—	—
23*	528	132	21	—	—	—	—	—	—
24*	353	91	10	—	—	—	—	—	—
25*	252	62	2	—	—	—	—	—	—
26	57	13	—	—	—	—	—	—	—
27	312	73	—	—	—	—	—	—	—
28	245	57	—	—	—	—	—	—	—
29	83	20	—	—	—	—	—	—	—
30	31	7	—	—	—	—	—	—	—
31	33	8	—	—	—	—	—	—	—
Total	34,672	8,110	336	8	3	1	3	3	1

[1] The sampling was done at Barbey Packing Corp. unloading dock. The days sampled are denoted by an asterisk. The entire catch was sampled for those days. The number of fish landed at Barbey on the days not sampled was estimated by using an average weight of 4.28 kg/fish which was calculated by dividing 23,417 kg sampled by 5,477 fish sampled.

TABLE 5.–Sex composition and average size of LV- and RV-marked 1968-brood coho salmon sampled during the 1971 Youngs Bay gill-net season.

Mark	Number of fish	Average size		Sex of fish	
		Length (cm)	Weight (kg)	Male	Female
LV	303	67	3.9	120	183
RV	7	70	4.2	5	2
Total	310	67	3.9	125	185

TABLE 6.–Estimated catch of 1968-brood LV- and RV-marked coho salmon by year, area, and fishery, 1970 and 1971.[1]

Area and fishery	1970		1971	
	LV	RV	LV	RV
Youngs Bay gill net	5	0	498	12
Youngs Bay sport	0	0	—	—
Columbia River gill net	8	2	267	1,162
Total	13	2	765	1,174

[1] Columbia River and ocean sport and ocean commercial fisheries were not sampled for these marks.

DISCUSSION

Hatchery returns (see Table 3) indicate that there is little straying of the LV-marked coho salmon released in Youngs Bay to hatcheries in the area or back to the parent hatchery (Little White Salmon). Only five LV-marked fish were recovered at the four hatcheries near Youngs Bay. Only 4 LV-marked coho returned to Little White Salmon Hatchery in 1970 and 1971, while 355 RV-marked fish returned to the hatchery.

Catches of marked coho also suggest that they home to the area of release (Table 6). An estimated 504 LV-marked coho were caught in the Youngs Bay gill-net fishery in 1970 and 1971. Only 12 RV-marked fish were estimated to have been caught in the bay. For 1970 and 1971 combined, the estimated Columbia River gill-net catch of LV- and RV-marked coho was 267 and 1,162, respectively. Of the 267 LV coho caught, about 45% were taken in Zone 1; 30% in Zone 2; and 25% in Zones 3 through 5. This means that about 75% of the LV-marked coho caught in the Columbia River were caught in waters adjacent to Youngs Bay. Since few LV-marked fish returned to Little White Salmon Hatchery or hatcheries in the area, it is reasonable to assume that these fish were bound or searching for the area of release.

These catches and hatchery returns gave an indication that the coho homed to the area of release with little straying. With few exceptions, the LV-marked coho released in Youngs Bay returned to the Youngs Bay area, and the RV-marked coho released at Little White Salmon Hatchery were bound for or returned to the hatchery.

Other investigators have reported various degrees of straying and homing tendencies of transported fish. Ellis and Noble (1960) reported returning fall chinook salmon from Klickitat Salmon Hatchery released in the lower Columbia River showed a greater tendency to stray than chinook released at the hatchery. Few of the transported chinook returned to the hatchery.

Wagner (1969) found that steelhead trout smolts trapped on the Alsea River and transported downstream returned as adults to an upstream trap in fewer numbers than untransported steelhead trout. This was probably due to the transported steelhead straying into tributaries as they moved upstream. From this and other studies (Wagner 1967), he concluded that the homing imprint in definitely influenced by stocking site and that capturing and transferring smolts during their downstream migration may cause gaps in imprinting. These gaps could result in delayed adult upstream migration. The duration of the delay probably depends on the strength of upstream stimuli.

Experiments conducted at hatcheries in Oregon, Washington, and California have shown that a majority of the chinook salmon, coho salmon, or steelhead trout released as smolts in an area with no downstream migration prior to hauling return to the area of release as adults. Studies at Ice Harbor Dam on the Snake River, 538 km above the Columbia River mouth (334 miles), indicated that chinook transported from Ice Harbor to below Bonneville Dam, a distance of 304 km (189 miles), returned as adults to Ice Harbor with little straying (Ebel et al. 1972).

These studies and our data suggest that coho salmon released in an area to create or enhance a fishery would home back to that area.

When examining the contribution of the RV- and LV-marked coho salmon to the fisheries sampled, it appears that the RV group released at Little White Salmon Hatchery had better survival than the LV group released at Youngs Bay. The total catch of RV-marked 1968-brood coho in 1970 and 1971 was 1,176 or 11.7 per 1,000 released compared to 778 LV coho caught or 7.7 per 1,000 released. However, a good comparison between the recoveries of the two groups cannot be made because of incomplete sampling. The ocean fisheries and Columbia River sport fishery were not sampled for LV- or RV-marked coho, and the Youngs Bay sport fishery was sampled only sparsely in 1970. Catches of LV- and RV-marked fish in these fisheries could alter the contribution of either or both groups significantly.

A good comparison of the contribution of the two groups is also hampered by the difference in size and time of release of the groups. The LV-marked coho were released in Youngs Bay on 23, 27, and 29 April 1970, at 49.9 fish/kg (22.6/pound). The RV-marked coho were released at Little White Salmon Hatchery 2 wk later on 12 May and at a larger size, 40.1 fish/kg (18.2/pound). This later release of larger fish could have improved the survival of the RV-marked coho.

A third factor inhibiting comparisons of the contributions of the RV and LV groups is hauling mortality. Tests have indicated that post-transport mortality may have a noteworthy effect on transported fish (Ebel et al. 1972). It is not known if the procedures used in this study to transport fish to Youngs Bay were more or less detrimental than the more natural migration pattern from the hatchery through Bonneville Dam and downstream to the ocean. If the employed transportation method caused significant mortalities and if changes in the method can be made to improve survival, then a better contribution from this type of release procedure could be obtained.

Other researchers have had similar difficulties in evaluating groups of fish released at different sites. Ellis and Noble (1960) had difficulty comparing the contribution and survival of groups of chinook salmon released at Klickitat Hatchery and Skamokawa, Wash., 354 km (220) and 53 km (33 miles), respectively, from the Columbia River mouth. Differences in the size of fish at release and marks used on each group as well as generally poor nutrition and survival during the hatchery rearing period influenced the results. However, the catch data indicate that contribution to the Columbia River fisheries was increased by release site manipulation. If straying could have been evaluated, total survival for the transported group may have been greater than the nontransported fish.

Wagner (1967, 1969) noted in studies with various release sites for steelhead on the Sandy, Alsea, and Wilson rivers that, in general, the contribution of hatchery reared steelhead to the sport fisheries was increased by releasing smolts in the lower stream areas. Here again, different mark types on the groups and variations in fishing effort on different stream sections may have influenced the results.

More recently Ebel et al. (1972) transported chinook salmon around Snake and Columbia River dams. They found that the contribution ratio of transported versus nontransported fish in the lower Columbia River sport and commercial fisheries was 1.4 to 1. Passage of chinook smolts through Snake and Columbia River dams certainly had an influence on survival differences between transported and nontransported groups.

SUMMARY AND CONCLUSIONS

This study was initiated to determine the feasibility of creating or enhancing a fishery in a specific area by releasing hatchery salmon smolts into that area. The plan was to release hatchery coho salmon smolts into an area and sample the fisheries in the area to determine if the fish returned in great enough numbers to warrant expansion of this practice.

Two groups of approximately 100,000 1968-brood coho at Little White Salmon National Fish Hatchery were marked—one with a right ventral finclip and the other with a left ventral finclip. Youngs Bay near Astoria, Oreg., was selected as the release site for the LV-marked group. The RV-marked coho were released at the hatchery. The releases were made in April and May of 1970.

The Youngs Bay and Columbia River gill-net fisheries were sampled for these marks in the fall of 1970 and 1971. A comparison of the catches and hatchery returns of the two groups showed that the two groups homed back to their respective areas of release with very little straying. The contribution of these two groups to the fisheries sampled was 7.7 fish per 1,000 released for the LV-marked Youngs Bay release and 11.7 fish per 1,000 released for the RV-marked Little White Salmon Hatchery release.

These statistics appear to favor the Little White Salmon Hatchery release, but there are several factors which prevent an accurate comparison of the two groups. First, the LV-marked coho were released in Youngs Bay 2 wk prior to and at a smaller size than the RV-marked coho released at the hatchery. Second, no evaluation was made of the possible effects of delayed mortalities of the LV coho due to hauling. Third, incomplete sampling for these marks was carried out in the ocean sport and commercial fisheries. Finally, duplication of single fin marks in the ocean fisheries prevented assignments to specific experiments. These four factors could have a significant influence on the contribution of either or both groups of coho.

Conclusions as to the practicality of transporting fish to an area to create or enhance local fisheries cannot be reached because of the four unknown factors influencing contribution. However, catches, hatchery returns, and the lack of straying indicate that this practice is biologically feasible. A study structured to evaluate the total contribution of two releases similar to those in this investigation and to eliminate the unknowns is presently underway.

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LITERATURE CITED

Ebel, W. J., D. L. Park, and R. C. Johnsen.
1972. Effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. Fish. Bull., U.S. 71:549-563.

Ellis, C. H., and R. E. Noble.
1960. Barging and hauling experiments with fall chinook salmon on the Klickitat River to test effects on survivals. Wash. Dep. Fish., 70th Annu. Rep.:57-71.

Groves, A. B., G. B. Collins, and P. S. Trefethen.
1968. Roles of olfaction and vision in choice of spawning site by homing adult chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 25:867-876.

Hasler, A. D.
1966. Underwater guideposts; homing of salmon. Univ. Wis. Press, Madison, 155 p.

Hasler, A. D., and W. J. Wisby.
1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. Am. Nat. 85:223-238.

Taft, A. C., and L. Shapovalov.
1938. Homing instinct and straying among steelhead trout (*Salmo gairdnerii*) and silver salmon (*Oncorhynchus kisutch*). Calif. Fish Game 24:118-125.

Wagner, H. H.
1967. A summary of investigations of the use of hatchery-reared steelhead in the management of a sport fishery. Oreg. State Game Comm., Fish. Rep. 5:1-62.
1969. Effect of stocking location of juvenile steelhead trout, *Salmo gairdnerii*, on adult catch. Trans. Am. Fish. Soc. 98:27-34.

Weiss, E. F.
1966. The coho salmon fishery of Youngs Bay, Oregon. Fish Comm. Oreg., Res. Briefs 12(1):52-57.

Wisby, W. J., and A. D. Hasler.
1954. Effect of olfactory occlusion on migrating silver salmon (*O. kisutch*). J. Fish. Res. Board Can. 11:472-478.

MESOPELAGIC MICRONEKTON IN HAWAIIAN WATERS: FAUNAL COMPOSITION, STANDING STOCK, AND DIEL VERTICAL MIGRATION

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ABSTRACT

On one cruise off leeward Oahu, Hawaii, micronekton from 9 deep-oblique mid-water trawl tows (0-1,200 m) and a 24-h series of 14 consecutive shallow-oblique tows (0-400 m) were sorted into 16 faunal groups, enumerated, and weighed. Diel-related trawl avoidance was not significant in deep tows. Mean total micronekton standing stocks for the deep tows were 898 organisms/100 m^2 ocean surface and 494 g (wet weight)/100 m^2 ocean surface. Fishes comprised half of the total numbers and biomass, while crustaceans contributed one-third of the total numbers and one-fifth of the biomass. Of the micronekton deeper than 400 m during the day, 43% of the number of organisms with 47% of the biomass migrated into the upper 400 m at night.

Micronekton play important roles in the oceanic ecosystem, yet few studies have examined the whole fauna in one area to measure standing stock, percent standing stock involved in diel vertical migration, or the relative contributions of major groups to the standing stock. This study considers such data taken on one cruise off Hawaii in the fall of 1972.

Samples were taken over 2,500-m deep waters 10-25 km off the leeward (west) coast of Oahu, in the Hawaiian Archipelago (approximately between lat. 21°15′N, long. 158°15′W and lat. 21°30′N, long. 158°22′W). Physical, chemical, and microbiological data are available for the sampling area (Schuert 1970; Gundersen et al. 1972) and nearby Station Gollum (lat. 22°10′N, long. 158°00′W) (Gordon 1970, 1971). A broad thermocline about 50-500 m deep is present throughout the year (Figure 1). A salinity minimum of 34.0‰ occurs at 400-500 m and a maximum of about 35.2‰ occurs around 100 m (Gordon 1970). The oxygen concentration varies from a minimum of 0.7 ml O_2/liter at 600-800 m to a maximum of about 5.3 ml O_2/liter at the surface (Gordon 1970). Water transparency is very high. In August 1972, noon irradiance measurements at a nearby station, lat. 28°29′N, long. 155°14′W, dropped from a surface level of 7×10^2 $\mu W/cm^2$ (at 471 nm) to 1.8×10^{-3} $\mu W/cm^2$) at 471 nm) 400 m deep, $k = 0.029$ below 200 m (F. M. Kampa, pers. commun.) (cf. G. L. Clarke 1971:43). Primary productivity in this area has been estimated at 50 g C/m^2-yr (S. A. Cattell, pers. commun.). The mean seasonal standing stock of zooplankton in the upper 200-m layer off Oahu is about 2.6 g (wet weight)/m^2 (Nakamura 1967).

GEAR AND METHODS

Trawl

All samples were taken with a 10-foot (3-m) Isaacs-Kidd Mid-water Trawl (IKMT) of standard design (Devereaux and Winsett 1953). The anterior portion of the net was lined with 6.35-mm (stretch) knotless nylon mesh; the middle portion was lined with 4.75-mm knotless nylon mesh; and the cod end was a 1.0-m diameter plankton net of 0.333-mm Nitex[2] mesh. Water flow was measured with a flowmeter (General Oceanics 2030) suspended near the center of the mouth, about 1 m inside the net. A time-depth recorder (TDR) (Benthos 1170-1000 or -2500) provided data on the sampling path.

Trawling Method

All samples were taken on cruise TEUTHIS-18

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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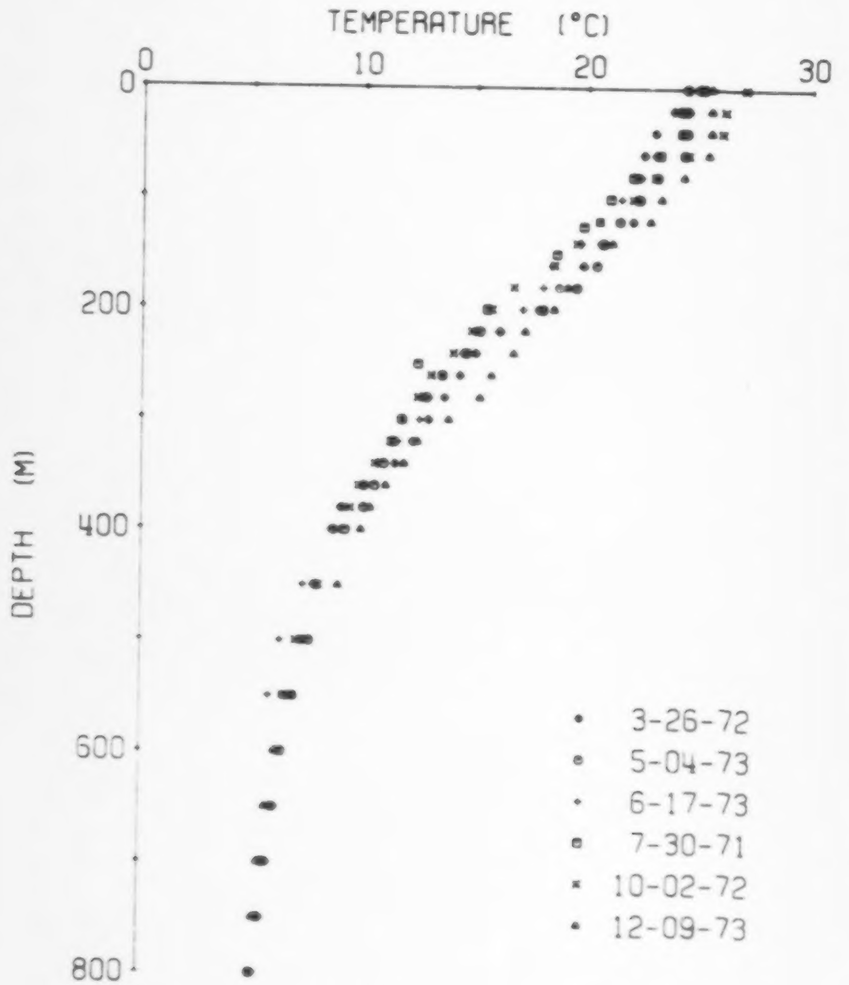

FIGURE 1.—Temperature-depth profiles taken by expendable bathythermographs in the sampling area.

on the University of Hawaii RV *Teritu*, 29 September to 3 October 1972 (Table 1). Sunrise occurred at about 0630 h, sunset at 1830. The moon was in its last quarter; on the last day of the cruise it rose at 0330 and set at about 1530.

All hauls were oblique and sampled primarily during descent. Two types of tows were made: deep tows 0-ca. 1,200 m (Figure 2a) and shallow tows 0-ca. 400 m (Figure 2b). Two deep-tow series (four day tows, five night tows total) were separated by a 24-h shallow-tow series (six day tows, six night tows); three twilight tows (no. 180, 184, 197) were also made, but the data were not included in computations of mean standing stocks. The two types of tows were designed to complement each other and provide data on diel vertical migrations; the two deep series were intended to examine day-to-day catch variability. The sampling depths were based on the results of previous horizontal sampling which indicated that nearly all micronekton resided between 400 and 1,200 m during the day.

TABLE 1.—Tow data for TEUTHIS-18.

Tow number	Date	Local time Begin	Local time End	Number flowmeter revolutions	Max. depth (m)
180	9/29	1703	2025	517,814	1,350
181		2040	0213	998,460	1,500
182	9/30	0235	0408	290,325	365
183		0657	1203	1,061,855	1,160
184		1221	1710	841,941	1,250
185		1912	0002	884,407	1,320
186	10/1	0015	0500	872,342	1,350
187		0522	0657	399,056	390
188		0716	0851	307,434	400
189		0904	1040	336,306	400
190		1051	1220	284,953	400
191		1236	1408	346,136	500
192		1429	1607	307,172	405
193		1620	1751	306,759	410
194		1758	1928	275,434	400
195		1937	2110	295,355	400
196		2117	2250	284,199	395
197		2257	0029	293,163	440
198	10/2	0036	0210	274,276	415
199		0232	0409	308,441	420
200		0421	0554	305,249	400
201		0630	1117	935,456	1,200
202		1134	1612	844,093	1,240
203		1856	2330	857,374	1,310
204		2340	0434	935,631	1,210

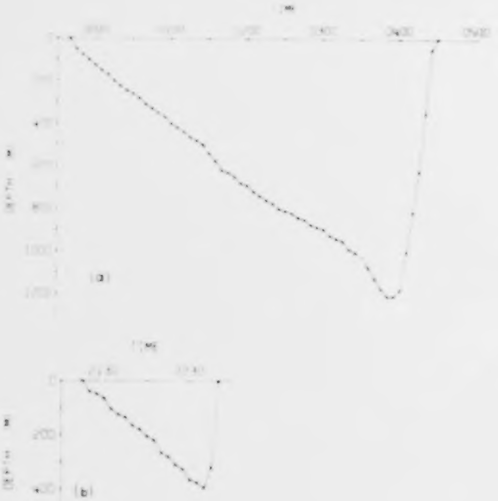

FIGURE 2.—Time-depth records for typical tows, depth plotted every 5 min. a. Deep tow, no. 204. b. Shallow tow, no. 196.

A stepped sampling strategy was adopted. The ship speed was 100 m/min (3.5 knots) for all sampling except during retrieval when the ship was nearly stopped. For the shallow tows, 100 m of cable were let out at 50 m/min every 5 min until 1,100 m of cable were out. This placed the trawl at about the 400-m depth. After 5 min at this depth, the trawl was retrieved as fast as possible. Total duration of shallow tows was about 1.5 h, that of the retrieval phase about 0.3 h. For deep tows, the first 1,100 m of cable were let out in the same manner as for the shallow tows. Beyond 1,100 m, 200 m of cable were let out at 50 m/min every 10 min until 3,400 m of cable were out. After 10 min at this depth (about 1,200 m), the trawl was retrieved as fast as possible. Total duration of deep tows was about 5 h; retrieval took about 1 h. The distribution of mean sampling times in each 100-m depth interval is shown in Table 2. By inspection, the variability seemed small enough to treat all tows within each type equally.

TABLE 2.—Distribution of mean sampling time per tow (minutes) and standard deviation (SD) with depth.

Sample depth interval (m)	Shallow				Deep			
	Day (6 tows)		Night (7 tows)		Day (4 tows)		Night (5 tows)	
	Mean time/tow (min)	SD	Mean time/tow (min)	SD	Mean time/tow (min)	SD	Mean time/tow (min)	SD
0-100	21.0	0.0	21.3	1.4	19.3	4.9	17.4	3.2
101-200	22.0	1.4	21.3	1.0	20.3	6.7	17.8	2.8
201-300	21.5	1.7	22.2	2.4	24.3	0.6	21.4	3.9
301-400	26.0	1.4	25.2	3.1	26.0	4.6	28.4	3.8
>400	3.5	0.5	2.7	4.6				
0-400	94.7	2.7	92.9	2.3	90.0	7.9	89.0	4.5
401-500					24.7	3.1	25.0	2.1
501-600					24.7	11.6	18.8	4.4
601-700					23.0	1.7	29.6	4.4
701-800					22.3	2.8	21.8	2.7
801-900					39.7	7.1	34.0	5.6
901-1,000					23.7	7.8	20.6	5.6
1,001-1,100					17.7	8.6	14.8	2.4
1,101-1,200					19.7	14.4	13.4	3.5
1,201-1,300					10.7	9.7	11.0	2.0
1,301-1,400					0.0		10.6	7.2
1,401-1,500					0.0		7.4	16.6
Total					291.0	13.7	292.0	23.3

Sample Processing

For this study, micronekton was defined as the pelagic marine animals longer than 1 cm caught by the 10-foot IKMT with the trawling methods described above. Each catch was preserved in buffered 7% seawater-Formalin. The animals were originally sorted to family or genus but subsequently were lumped into larger groups chosen to roughly discriminate between vertical migrators and non-migrators, as well as among trophic groups (Table 3). Group names are capitalized in the text. All micronekton except siphonophores were counted, and all groups were weighed (blotted wet weight ±0.01 g). Siphonophore biomass was included in the Cnidaria group, but the

TABLE 3.–Group composition used to sort each catch.

1. Myctophidae.
2. *Cyclothone* (Gonostomatidae).
3. Other Gonostomatidae.
4. Sternoptychidae.
5. Other Stomiatoidei: Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Melanostomiatidae, Stomiatidae.
6. Anguilliformes: Cyemidae, Eurypharyngidae, leptocephali, Nemichthyidae, Serrivomeridae.
7. Miscellaneous fishes: Alepisauridae, Apogonidae, Bathylagidae, Bregmacerotidae, Brotulidae, Ceratioidei, Cetomimidae, Chiasmodontidae, Evermanellidae, Giganturidae, Macrouridae, Melamphaeidae, Neoscopelidae, Omosudidae, Opisthoproctidae, Paralepididae, Scorpaenidae, Trachipteridae, Zeidae, Zoarcidae, larval neritic, unidentified larval midwater.
8. Caridea: Oplophoridae, Pandalidae, Pasaphaeidae.
9. Penaeidea: Penaeidae, Sergestidae.
10. Euphausiacea: Bentheuphausidae, Euphausiidae.
11. Mysidacea: Eucopeidae, Lophogastridae.
12. Miscellaneous Crustacea: Amphipoda, Isopoda, Ostracoda.
13. Cephalopoda.
14. Tunicata: Pyrosomidae, Salpidae.
15. Cnidaria: Hydrozoa, Scyphozoa, Siphonophora.
16. Miscellaneous invertebrates: Annelida, Ctenophora, Heteropoda, Pteropoda, Nemertea.
17. Zooplankton: Copepoda, larval Stomatopoda, other meroplankton, organisms ≤ 1 cm, residue.

Pooled classifications
Total fishes = Groups 1-7.
Total Crustacea = Groups 8-12.
Other invertebrates = Groups 14-16.
Total micronekton = Groups 1-16.

number of siphonophores could not be determined from the assorted zooids (Pugh 1974), and the numerical standing stock of Cnidaria is thus slightly underestimated. Organisms larger than 10 g/individual were weighed separately, but their weights and abundance were included in group totals. Most animals with greatest linear dimensions of about 1 cm or less, such as the euphausiid *Stylocheiron* spp., were placed into the zooplankton group although some sergestids in this size range were included in Penaeidea. Standing stocks of zooplankton shrimps were calculated from subsamples (Folsom splitter) of one deep tow.

Calculations

The volume of water filtered by each tow was determined by multiplying the distance travelled (as determined by the flowmeter) by the area of the net mouth. Mouth areas from 7.08 to 8.19 m² have been reported for the 10-foot IKMT (Brooks et al. 1974). We used 7.7 m² for our trawl. Zooplankton biomass was calculated for a mouth area of 7.7 m², the full IKMT mouth, and 0.785 m², the area of the cod end mouth. The true zooplankton concentration probably lies somewhere between these values because the anterior portions of the trawl funnel some zooplankton into the cod end while others pass through the meshes (Banse and Semon 1963; Hopkins 1966; Friedl 1971).

To calculate the number of organisms or biomass of each group per 100 m² of ocean surface, the catch was divided by the volume of water filtered; this quotient was multiplied by the maximum depth of the tow and the product was then multiplied by 100. This computation assumes all depths were sampled equally.

RESULTS

Standing Stock

The standing stocks from deep-day and deep-night tows were not significantly different (t-test, $P<0.05$) in either number of organisms or biomass for most groups, including total micronekton. Only the numbers of miscellaneous fishes and Mysidacea showed significant diel differences. Likewise there were no significant differences ($P<0.05$) between the two series of deep tows (tows 183-186 vs. 201-204). Consequently we treated all deep tows as replicates and pooled the data to compute mean micronekton standing stocks for the 0- to 1,200-m deep water column (Tables 4, 5). Shallow-day (tows 188-193) and shallow-night (tows 182, 195-200) data were obviously different and were treated separately in these tables. The percentage composition of the fauna by group is illustrated in Figure 3 for each of the three classes of tows.

The mean standing stocks of total micronekton for the 0- to 1,200-m water column are about 900 organisms and 500 g wet weight/100 m² of ocean surface (Tables 4, 5). Fishes comprised over one-half of both the total numbers and biomass; crustaceans constituted about one-third of the numbers and one-fifth of the biomass, while the cephalopods contributed only one-hundredth of the numbers but one-tenth of the biomass (Tables 4, 5). *Cyclothone* were more than twice as numerous as any of the other 15 groups, totalling almost 35% of the individuals caught (Figure 3a). The distribution of biomass among the groups varied less than the distribution of the abundance. No group contributed more than the Myctophidae which comprised 13% of total biomass (Figure 3a). A comparison of group rank by biomass with rank by abundance indicates that most of the more

TABLE 4.–Micronekton standing stock, mean number of organisms per 100 m^2 ocean surface. Standard deviation in parentheses.

Group	0-1,200 m		Day 0-400 m		Night 0-400 m	
Myctophidae	108.13	(45.71)	1.02	(1.15)	80.72	(22.65)
Cyclothone	308.29	(103.34)	6.07	(8.84)	19.48	(39.01)
Other Gonostomatidae	25.77	(3.70)	3.25	(3.84)	22.13	(8.56)
Sternoptychidae	22.97	(5.96)	0.42	(0.78)	4.36	(1.47)
Other Stomiatoidei	3.92	(2.04)	0.00		2.68	(1.70)
Anguilliformes	11.43	(4.46)	2.64	(1.04)	2.96	(2.23)
Misc. fishes	27.49	(7.64)	16.31	(5.08)	21.08	(5.83)
Caridea	40.18	(5.93)	1.70	(2.21)	27.52	(11.18)
Penaeidea	137.90	(34.99)	6.83	(3.74)	132.90	(21.68)
Euphausiacea	97.79	(28.16)	6.79	(5.77)	69.01	(11.50)
Mysidacea	9.89	(3.02)	0.00		8.73	(6.67)
Misc. Crustacea	4.08	(6.72)	0.00		1.88	(1.54)
Cephalopoda	8.44	(2.04)	3.60	(1.98)	5.95	(1.81)
Tunicata	28.05	(14.10)	50.26	(24.73)	25.01	(10.97)
Cnidaria	10.80	(9.41)	11.82	(2.49)	11.47	(8.81)
Misc. invertebrates	52.93	(25.02)	55.55	(7.73)	42.04	(10.03)
Total micronekton	898.07	(149.50)	166.27	(16.45)	477.94	(69.27)
Total fishes	508.00	(133.50)	29.71	(7.48)	153.41	(60.43)
Total Crustacea	289.84	(54.25)	15.32	(4.92)	240.04	(13.91)
Cepholopoda	8.44	(2.04)	3.60	(1.98)	5.95	(1.81)
Other invertebrates	91.78	(25.22)	117.63	(19.26)	78.52	(22.71)
No. organisms caught	12,037		1,576		5,136	
No. tows	9		6		7	

TABLE 5.–Micronekton standing stock, mean biomass, grams wet weight per 100 m^2 ocean surface. Standard deviation in parentheses.

Group	0-1,200 m		Day 0-400 m		Night 0-400 m	
Myctophidae	85.71	(20.36)	0.19	(0.17)	68.85	(12.26)
Cyclothone	45.91	(11.26)	0.45	(0.75)	1.20	(2.92)
Other Gonostomatidae	14.92	(8.48)	0.41	(0.48)	29.24	(25.22)
Sternoptychidae	25.05	(14.02)	0.39	(0.91)	7.45	(2.75)
Other Stomiatoidei	15.56	(12.53)	0.00		13.38	(14.73)
Anguilliformes	48.18	(43.65)	2.40	(3.04)	1.53	(1.63)
Misc. fishes	41.37	(40.16)	2.65	(0.93)	9.46	(6.35)
Caridea	50.49	(21.07)	0.15	(0.28)	30.27	(13.11)
Penaeidea	31.59	(10.61)	0.13	(0.10)	22.71	(3.88)
Euphausiacea	18.52	(3.98)	0.86	(0.80)	12.28	(1.57)
Mysidacea	8.80	(9.76)	0.00		4.42	(3.45)
Misc. Crustacea	1.09	(1.92)	0.00		1.09	(0.78)
Cephalopoda	48.71	(47.46)	2.02	(2.02)	13.84	(16.28)
Tunicata	34.07	(42.52)	5.90	(3.50)	21.68	(15.00)
Cnidaria	40.86	(46.86)	10.50	(5.50)	11.34	(12.87)
Misc. invertebrates	3.38	(3.49)	6.61	(2.35)	1.39	(0.33)
Total micronekton	494.20	(99.30)	32.68	(6.58)	251.11	(53.46)
Total fishes	256.70	(81.30)	6.50	(2.99)	132.09	(39.33)
Total Crustacea	110.49	(36.15)	1.14	(1.08)	70.77	(12.30)
Cephalopoda	48.71	(47.46)	2.02	(2.02)	13.84	(16.28)
Other invertebrates	78.31	(53.50)	23.01	(8.34)	34.41	(21.93)
Zooplankton[1]	48.12	(21.64)	15.24	(4.07)	49.20	(12.30)
Zooplankton[2]	471.95	(212.28)	149.45	(39.94)	482.57	(120.91)

[1] Calculated assuming 7.7 m^2 net mouth, full 10-foot IKMT mouth.
[2] Calculated assuming 0.785 m^2 net mouth, cod end mouth area.

abundant groups are comprised of small individuals (Figure 3a). Biomass estimates for zooplankton in deep tows ranged from about 10 to 100% of the total micronekton, depending on which mouth area was used for calculation (Table 5).

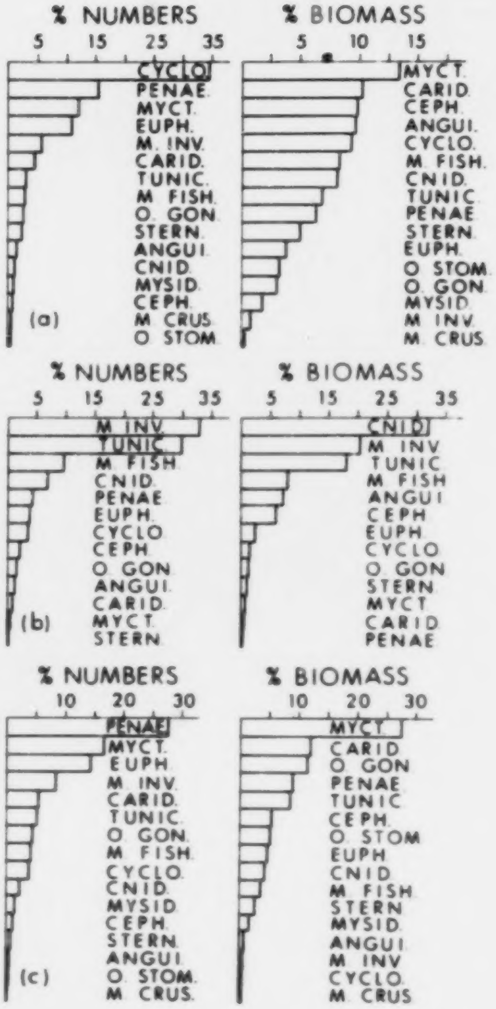

FIGURE 3.–Mean faunal composition by group as percent of total micronekton standing stock, number of organisms and wet-weight biomass. a. Deep-tows, 0-1,200 m. b. Shallow-day tows, 0-400 m. c. Shallow-night tows, 0-400 m. ANGUI. = Anguilliformes, CARID. = Caridea, CEPH. = Cephalopoda, CNID. = Cnidaria, CYCLO. = *Cyclothone*, EUPH. = Euphausiacea, M. CRUS. = Miscellaneous Crustacea, M. FISH. = Miscellaneous fishes, M. INV. = Miscellaneous invertebrates, MYCT. = Myctophidae, MYSID. = Mysidacea, O. GON. = Other Gonostomatidae, O. STOM. = Other Stomiatoidei, PENAE. = Penaeidea, STERN. = Sternoptychidae, TUNIC. = Tunicata.

The small euphausiids (<1 cm) which were sorted into the zooplankton group constituted 3.9 g wet weight and 831 individuals/100 m^2 ocean surface for one deep tow (no. 183). This is about nine times the mean abundance of micronektonic euphausiids, but only one-fifth of the mean euphausiid biomass.

To establish a rough index of the contribution of neritic and meroplanktonic animals to the pelagic catch for future comparison, the standing stock of stomatopod larvae (otherwise included in the zooplankton group (Table 5)) was compared to the total micronekton stock (Table 6). The stomatopod concentration is large relative to shallow-day micronekton catches but quite small with respect to shallow-night and especially to deep-tow catches.

TABLE 6.–Mean standing stock of stomatopod larvae expressed as percent of total micronekton standing stock per 100 m^2 of ocean surface, number of organisms and wet-weight biomass.

Item	0-1,200 m	Day 0-400 m	Night 0-400 m
Number (%)	4.3	58.3	11.4
Biomass (%)	0.6	12.9	2.9

Diel Vertical Migration

Because there were no significant differences between standing stock estimates of deep-day and deep-night tows, we concluded that any trawl avoidance was not due to diel factors and that increased shallow-night catches were primarily the result of vertical migration. Thus, the amount of vertically migrating micronekton was the difference between the shallow-day stock and the shallow-night stock (Tables 4, 5, 7). The percent migrating was then computed by dividing the amount migrating by the amount of micronekton deeper than 400 m during the day (deep-tow standing stock minus shallow-day stock). Percentages larger than 100 are considered sampling artifacts.

Of the total micronekton which resided deeper than 400 m during the day, 43% of the individuals with 47% of the biomass migrated into the upper 400 m at night (Table 7). This dramatic diel change in the catch rates of shallow tows is illustrated in Figures 4 and 5. The most numerous migrators were crustaceans, but most of the biomass was fishes. Between day and night tows the difference in composition of the 0- to 400-m layer of fauna is quite pronounced (Figure 3b, c).

The average weight per organism in each group for the 0- to 1,200-m deep water column was computed by dividing the mean group biomass in Table 5 by the mean number of organisms in the group shown in Table 4. The results are presented in Table 8 along with computations of the average biomass of individual migrators and non-migrators, based on the data in Table 7 and assuming that the non-migrator standing stock was the

TABLE 7.–Mean standing stock of vertically migrating micronekton, grams wet-weight biomass and number of organisms per 100 m^2 of ocean surface between 0 and 1,200 m, groups ranked by biomass and abundance. Percent migrating represents the portion of the group residing deeper than 400 m during the day which migrated into the 0- to 400-m layer at night.

Group	Biomass g / 100 m^2	Biomass % migr.	Group	Abundance No./ 100 m^2	Abundance % migr.
Myctophidae	69.66	106	Penaeidea	126.07	96
Caridea	30.12	60	Myctophidae	79.70	74
Other Gonostomatidae	28.83	199	Euphausiacea	62.22	68
Penaeidea	22.58	72	Caridea	25.82	67
Tunicata	15.78	56	Other Gonostomatidae	18.88	84
Other Stomiatoidei	13.36	86	Cyclothone	13.41	4
Cephalopoda	11.82	25	Mysidacea	8.73	88
Euphausiacea	11.42	65	Misc. fishes	4.77	43
Sternoptychidae	7.06	29	Sternoptychidae	3.94	17
Misc. fishes	6.81	18	Other Stomiatoidei	2.68	68
Mysidacea	4.42	50	Cephalopoda	2.35	49
Misc. Crustacea	1.09	100	Misc. Crustacea	1.88	46
Cnidaria	0.84	3	Anguilliformes	0.32	4
Cyclothone	0.74	2	Cnidaria	(1)	
Misc. invertebrates	(1)		Misc. invertebrates	(1)	
Anguilliformes	(1)		Tunicata	(1)	
Total fishes	125.59	50	Total Crustacea	224.72	82
Total Crustacea	69.63	64	Total fishes	123.70	26
Cephalopoda	11.82	25	Cephalopoda	2.35	49
Other invertebrates	11.40	21	Other invertebrates	(1)	
Total micronekton	218.43	47	Total micronekton	311.67	43

[1] 0-400-m day stock > 0-400-m night stock.

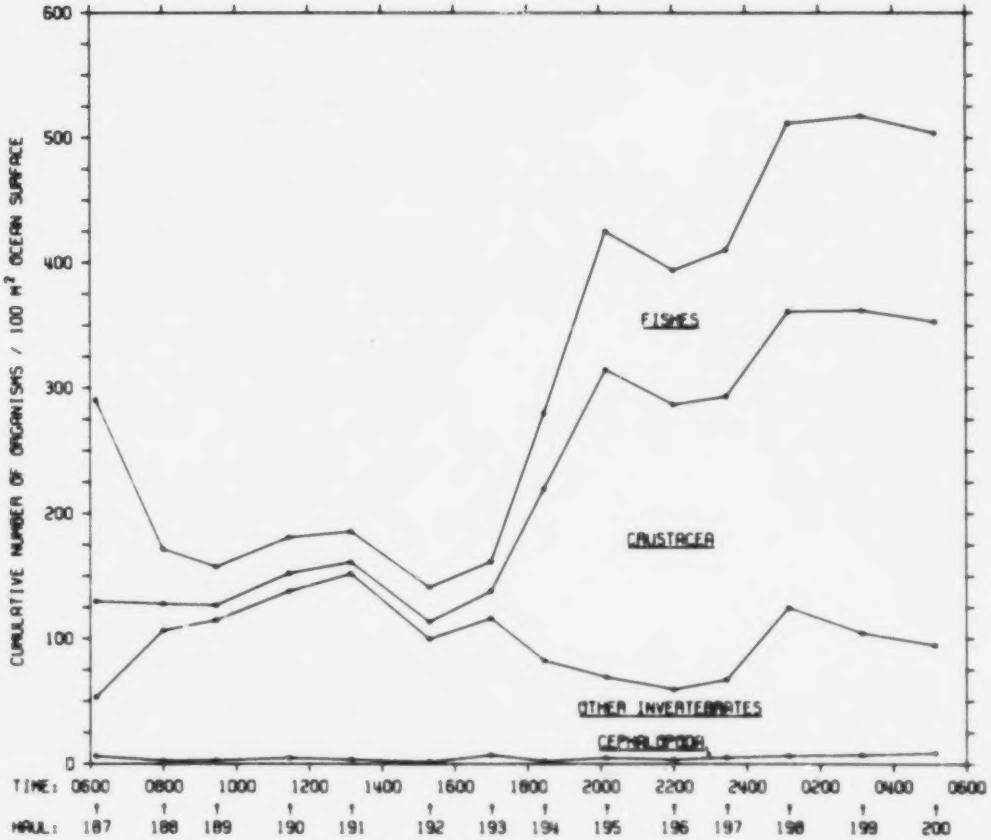

FIGURE 4.–Shallow-tow (0-400 m) standing stock of micronekton abundance over 24 h. Time is plotted for midpoint of each tow.

difference between the deep-tow stock and the migrator stock. In general, the average weight per migrating fish is greater than the weight of the non-migrators, while the opposite holds for the crustaceans and cephalopods, that is, the smaller-sized members of the groups migrate.

The occurrence of organisms larger than 10 g (wet weight) per individual was highly variable both with respect to abundance and biomass (Table 9). None occurred in the groups of *Cyclothone*, Sternoptychidae, Penaeidea, Euphausiacea, miscellaneous Crustacea, or miscellaneous invertebrates. The only large organism in shallow-day tows was one tunicate. In deep tows, large animals were less than 1% of the number of total micronekton but 30% of the biomass. With respect to biomass, about one-quarter of the total fishes, one-eighth of the total crustacea, four-fifths of the Cephalopoda and one-half of the other invertebrates were made up of individuals larger than 10 g each. In shallow-night tows these proportions are smaller for all groups except other invertebrates which is about the same.

DISCUSSION

Restrictions

The interpretation of our data must be considered with several restrictions. Larger, highly mobile micronekton, especially fishes and cephalopods, probably avoid or escape the trawl (Pearcy and Laurs 1966; M. R. Clarke 1969; T. A. Clarke 1973, 1974) resulting in underestimation of

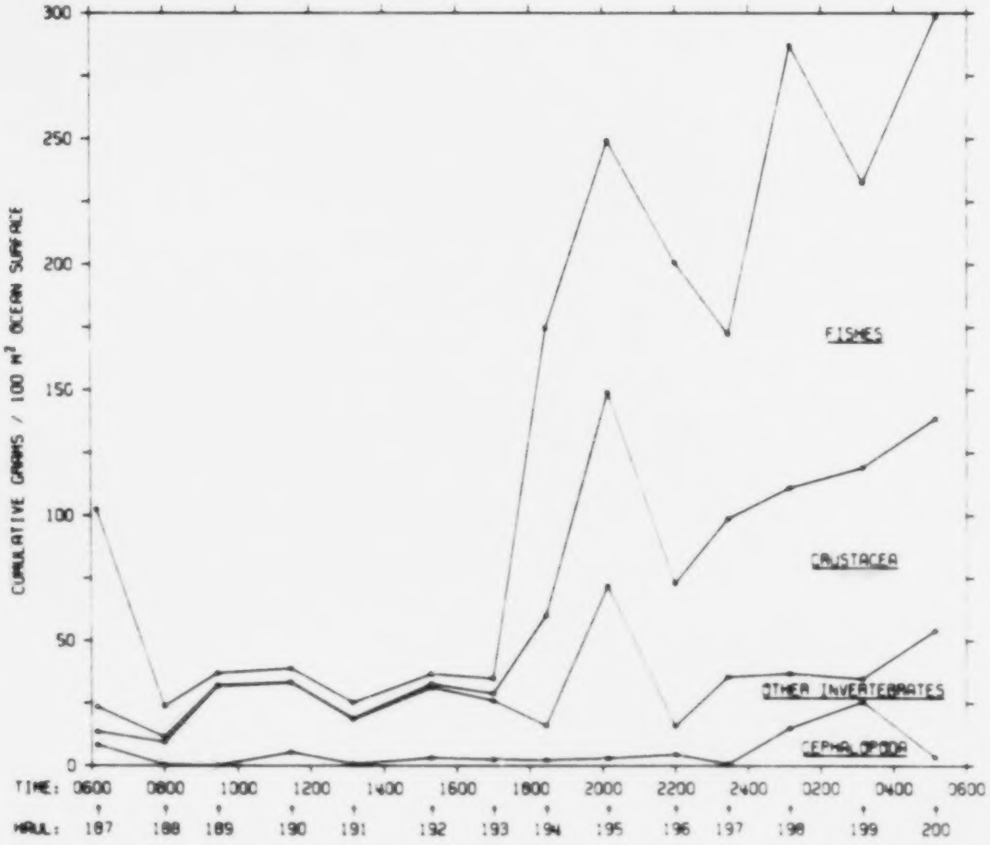

FIGURE 5.—Shallow-tow (0-400 m) standing stock of micronekton biomass (wet weight) over 24 h. Time is plotted for midpoint of each tow.

the numbers and especially biomass. In addition, pooling species into the 16 groups of Table 3 sometimes lumps vertical migrators with nonmigrators, and primary carnivores with higher predators, blurring a precise ecological definition for a group. We feel, however, that our groups are adequate for a first overview of the micronekton fauna off Hawaii.

Our data may not represent standing stocks characteristic of the open ocean, and the possibility of an island effect should be considered. Oahu affects surface circulation up to 1,500 km downstream (Barkley 1971), but effects on plankton and micronekton standing stocks are not clear. An island mass effect has been observed off Oahu for phytoplankton (Gilmartin and Revelante 1974). King and Hida (1954, 1957a, b) found little correlation between distance from Oahu and zooplankton standing stock, whereas other workers have found a decreasing standing stock with increasing distance from the island (Sette 1955; McGary 1955; Doty and Oguri 1956). Nakamura (1967) could detect no differences in mean zooplankton standing stock between windward and leeward Oahu samples, but windward samples consistently contained more decapods. We are not certain what island effects, if any, influence the leeward Oahu micronekton other than the occasional occurrence of some larvae of reef and benthic animals (e.g., stomatopods, crabs, fishes) which fall into the size range of micronekton as defined here.

Temporal fluctuations in micronekton standing stock pose an important caveat in evaluating our

TABLE 8.–Mean biomass per animal, grams wet weight, for the 0- to 1,200-m water column, vertical migrators (Table 7), and nonmigrators (animals residing deeper than 400 m at night).

Group	0-1,200 m	Migrators	Nonmigrators
Myctophidae	0.61	0.87	(1)
Cyclothone	0.15	0.06	0.34
Other Gonostomatidae	0.58	1.53	(1)
Sternoptychidae	1.09	1.79	0.95
Other Stomiatoidei	3.97	4.99	1.77
Anguilliformes	4.22	(2)	(2)
Misc. fishes	1.50	1.43	2.12
Caridea	1.26	1.17	1.42
Penaeidea	0.23	0.18	0.76
Euphausiacea	0.19	0.18	0.20
Mysidacea	0.89	0.51	3.77
Misc. Crustacea	0.27	0.59	(1)
Cephalopoda	5.77	5.03	6.06
Tunicata	1.21	(2)	(2)
Cnidaria	(3)	(3)	(3)
Misc. invertebrates	0.06	(2)	(2)
Total micronekton	0.55	0.70	0.47
Total fishes	0.51	1.01	0.34
Total Crustacea	0.38	0.31	0.63
Other invertebrates	(2, 3)	(2, 3)	(2, 3)

[1] 0- to 400-m night stock minus 0- to 400-m day stock ≥ 0- to 1,200-m stock.

[2] 0- to 400-m day stock > 0- to 400-m night stock.

[3] Siphonophores were not enumerated.

single-cruise data. In other parts of the world, investigators have reported seasonal biomass fluctuations of two- to sevenfold for some micronekton groups (Legand 1969; Blackburn et al. 1970; Tranter 1973), and abundance fluctuations of some species up to fifteen- to fortyfold (Pearcy 1964; Legand et al. 1970). Previous work in Hawaiian waters has demonstrated temporal variability in primary productivity (Gordon 1971:1132), epipelagic zooplankton standing stock (Nakamura 1967; Shomura and Nakamura 1969), and such mesopelagic micronekton as myctophids (T. A. Clarke 1973) and stomiatoids (T. A. Clarke 1974). The limited data available suggest at least twofold temporal fluctuations in micronekton standing stocks might be expected in Hawaiian waters. At this time we cannot predict seasonal oscillations in standing stock. Thus, until better seasonal data are available, our reported standing stock and faunal composition values should only tentatively be considered characteristic for Hawaii.

Standing Stock

On the basis of fish distributions, Amesbury (1975) has definied the 400- to 1,200-m depth range off Hawaii as the mesopelagic zone. Very few animals have been taken deeper than 1,200 m in opening-closing tows. Thus, standing stock values determined from our deep tows are probably reliable estimates for the micronekton of the whole water column except near-bottom waters.

In spite of the shortcomings, the data add considerably to our knowledge of micronekton especially because we sampled nearly the whole depth range of the fauna, used a fully lined net with small mesh, towed at a relatively high speed, sampled when the moon had a minimal effect on avoidance (cf. T. A. Clarke 1973), took several sample replicates, monitored sampling volume and depth, and determined standing stocks for all components of the catch. The general lack of diel-related avoidance agrees with the findings of T. A. Clarke (1973) and Atsatt and Seapy (1974) but is in contrast to the results of Pearcy and Laurs (1966).

TABLE 9.–Mean standing stock of micronekton larger than 10 g (wet weight)/individual, by group. *a*. No. organisms/100 m² ocean surface. *b*. Grams biomass/100 m² ocean surface. Standard deviation in parentheses.

a. Number Group	0-1,200 m		Day 0-400 m		Night 0-400 m	
Myctophidae	0.08	(0.22)	0.00		0.10	(0.26)
Other Gonostomatidae	0.15	(0.28)	0.00		0.38	(0.55)
Other Stomiatoidei	0.31	(0.36)	0.00		0.18	(0.32)
Anguilliformes	0.81	(0.83)	0.00		0.00	
Misc. fishes	0.56	(0.88)	0.00		0.00	
Caridea	0.53	(0.56)	0.00		0.09	(0.25)
Mysidacea	0.22	(0.49)	0.00		0.00	
Cephalopoda	0.54	(0.47)	0.00		0.27	(0.51)
Tunicata	0.83	(1.57)	0.10	(0.23)	0.54	(0.45)
Cnidaria	0.52	(1.16)	0.00		0.18	(0.49)
Total micronekton	4.62	(2.27)	0.10	(0.23)	1.76	(0.65)
Total fishes	1.97	(1.21)	0.00		0.67	(0.41)
Total Crustacea	0.76	(2.76)	0.00		0.09	(0.25)
Cephalopoda	0.54	(0.47)	0.00		0.27	(0.51)
Other invertebrates	1.35	(1.74)	0.10	(0.23)	0.73	(0.77)
No. organisms	61		1		19	
No. tows	9		6		7	

b. Biomass, grams/100 m² Group	0-1,200 m		Day 0-400 m		Night 0-400 m	
Myctophidae	1.08	(3.25)	0.00		1.08	(2.82)
Other Gonostomatidae	2.99	(6.41)	0.00		13.24	(20.52)
Other Stomiatoidei	9.38	(11.25)	0.00		7.77	(16.48)
Anguilliformes	26.60	(36.08)	0.00		0.00	
Misc. fishes	19.25	(37.84)	0.00		0.00	
Caridea	10.93	(12.41)	0.00		1.14	(3.01)
Mysidacea	3.06	(8.71)	0.00		0.00	
Cephalopoda	40.03	(49.24)	0.00		8.15	(15.80)
Tunicata	26.28	(12.95)	1.39	(11.54)	15.29	(14.[illegible])
Cnidaria	14.58	(35.30)	0.00		2.08	(7.11)
Total micronekton	153.98	(54.80)	1.39	(11.54)	49.34	(14.81)
Total fishes	58.31	(38.50)	0.00		22.08	(20.18)
Total Crustacea	13.77	(17.38)	0.00		1.14	(3.01)
Cephalopoda	40.03	(49.24)	0.00		8.15	(15.80)
Other invertebrates	40.86	(44.70)	1.39	(11.54)	17.98	(18.57)

We searched the literature for data to compare the standing stock and composition of micronekton off Hawaii with that of other regions. Few studies provided data from more than one sampling period; each used different gear and techniques, and all are subject to most of the restrictions cited previously. We feel that meaningful regional comparisons are premature until data on the temporal variability of the fauna are available from samples covering the entire depth range of the fauna.

Diel Vertical Migration

About one-half of the total micronekton wet-weight biomass in our study area appeared to migrate from day-depths greater than 400 m to night-depths shallower than 400 m. During the day, about 90% of the mean total micronekton standing stock biomass lived deeper than 400 m (Tables 5, 7). Because most vertically migrating fishes have a lower water content than nonmigrators (Childress and Nygaard 1973) the percent of total micronekton dry weight which migrates would be even higher. The same probably holds for cephalopods. If migrators have shorter life spans and higher metabolic rates than nonmigrators (cf. Childress and Nygaard 1973; T. A. Clarke 1973; Meek and Childress 1973), then the percent of the annual micronekton production represented by migrating animals would be especially high.

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LITERATURE CITED

AMESBURY, S. S.
1975. The vertical structure of the micronektonic fish community off leeward Oahu. Ph.D. Thesis, Univ. Hawaii.

ATSATT, L. H., AND R. R. SEAPY.
1974. An analysis of sampling variability in replicated midwater trawls off southern California. J. Exp. Mar. Biol. Ecol. 14:261-273.

BANSE, K., AND D. SEMON.
1963. On the effective cross-section of the Isaacs-Kidd midwater trawl. Univ. Wash. Dep. Oceanogr., Tech. Rep. 88, 9 p.

BARKLEY, R. A.
1971. Island wakes and their effects. Pac. Sci. Congr. Proc. 12(1):145.

BLACKBURN, M., R. M. LAURS, R. W. OWEN, AND B. ZEITSCHEL.
1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. (Berl.) 7:14-31.

BROOKS, A. L., C. L. BROWN, JR., AND P. H. SCULLY-POWER.
1974. Net filtering efficiency of a 3-meter Isaacs-Kidd midwater trawl. Fish Bull., U.S. 72:618-621.

CHILDRESS, J. J., AND M. H. NYGAARD.
1973. The chemical composition of midwater fishes as a function of depth of occurrence off southern California. Deep-Sea Res. 20:1093-1109.

CLARKE, G. L.
1971. Light conditions in the sea in relation to the diurnal vertical migrations of animals. *In* G. B. Farquhar (editor), Proceedings of an international syposium on biological sound scattering in the ocean, p. 41-50. Maury Cent. Ocean Sci., Wash., D.C.

CLARKE, M. R.
1969. Cephalopoda collected on the SOND cruise. J. Mar. Biol. Assoc. U.K. 49:961-976.

CLARKE, T. A.
1973. Some aspects of the ecology of laternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.
1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 72:337-351.

DEVEREAUX, R. F., AND R. C. WINSETT.
1953. Isaacs-Kidd midwater trawl, final report. Scripps Inst. Oceanogr., Oceanogr. Equip. Rep. 1, 18 p.

DOTY, M. S., AND M. OGURI.
1956. The island mass effect. J. Cons. 22:33-37.

FRIEDL, W. A.
1971. The relative sampling performance of 6- and 10-foot Isaacs-Kidd midwater trawls. Fish. Bull., U.S. 69:427-432.

GILMARTIN, M., AND N. REVELANTE.
1974. The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. J. Exp. Mar. Biol. Ecol. 16:181-204.

GORDON, D. C., JR.
1970. Chemical and biological observations at Station Gollum, an oceanic station near Hawaii, January 1969 to June 1970. Hawaii Inst. Geophys., Tech. Rep. HIG-70-22, 44 p.
1971. Distribution of particulate organic carbon and nitrogen at an oceanic station in the central Pacific. Deep-Sea Res. 18:1127-1134.

Gundersen, K., C. W. Mountain, D. Taylor, R. Ohye, and J. Shen.
1972. Some chemical and microbiological observations in the Pacific Ocean off the Hawaiian Islands. Limnol. Oceanogr. 17:524-531.

Hopkins, T. L.
1966. A volumetric analysis of the catch of the Isaacs-Kidd midwater trawl and two types of plankton nets in the Antarctic. Aust. J. Mar. Freshwater Res. 17:147-154.

King, J. E., and T. S. Hida.
1954. Variations in zooplankton abundance in Hawaiian waters, 1950-52. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 118, 66 p.
1957a. Zooplankton abundance in Hawaiian waters, 1953-1954. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 221, 23 p.
1957b. Zooplankton abundance in the central Pacific. Part II. U.S. Fish Wildl. Serv., Fish Bull. 57:365-395.

Legand, M.
1969. Seasonal variations in the Indian Ocean along 110°E. VI. Macroplankton and micronekton biomass. Aust. J. Mar. Freshwater Res. 20:85-103.

Legand, M., P. Bourret, R. Grandperrin, and J. Rivaton.
1970. A preliminary study of some micronektonic fishes in the equatorial and tropical western Pacific. *In* W. S. Wooster (editor), Scientific exploration of the south Pacific, p. 226-235. Natl. Acad. Sci., Wash., D.C.

McGary, J. W.
1955. Mid-Pacific oceanography, Part IV. Hawaiian offshore waters, December 1949-November 1951. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 152, 138 p.

Meek, R. P., and J. J. Childress.
1973. Respiration and the effect of pressure in the mesopelagic fish *Anoplogaster cornuta* (Beryciformes). Deep-Sea Res. 20:1111-1118.

Nakamura, E. L.
1967. Abundance and distribution of zooplankton in Hawaiian waters, 1955-56. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 544, 37 p.

Pearcy, W. G.
1964. Some distributional features of mesopelagic fishes off Oregon. J. Mar. Res. 22:83-102.

Pearcy, W. G., and R. M. Laurs.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

Pugh, P. R.
1974. The vertical distribution of the siphonophores collected during the SOND cruise, 1965. J. Mar. Biol. Assoc. U.K. 54:25-90.

Schuert, E. A.
1970. Turbulent diffusion in the intermediate waters of the north Pacific Ocean. J. Geophys. Res. 75:673-682.

Sette, O. E.
1955. Considerations of midocean fish production as related to oceanic circulatory systems. J. Mar. Res. 14:398-414.

Shomura, R. S., and E. L. Nakamura.
1969. Variations in marine zooplankton from a single locality in Hawaiian waters. U.S. Fish Wildl. Serv., Fish. Bull. 68:87-100.

Tranter, D. J.
1973. Seasonal studies of a pelagic ecosystem (meridian 110° E). *In* B. Zeitzschel (editor), The biology of the Indian Ocean, p. 487-520. Springer-Verlag, N.Y.

DESCRIPTION AND BIOLOGY OF A NEW SPECIES OF PELAGIC PENAEID SHRIMP, *BENTHEOGENNEMA BURKENROADI*, FROM THE NORTHEASTERN PACIFIC[1]

Earl E. Krygier[2] and Robert A. Wasmer[3]

ABSTRACT

The new species of pelagic penaeid shrimp lacks the richly plumose arthrobranch described for the genus and has a single pair of terminal spines on the telson. It is found mainly in transitional water of the North Pacific between 500 and 1,000 m by day and 150 and 1,000 m at night. Examination of testes and ovaries, and the structures of the petasma and thelycum, indicates a 4-5 mo spawning season and an equal male to female sex ratio. Generation time was estimated to be 2 yr.

This paper describes the systematics and biology of a new species of pelagic penaeid shrimp of the genus *Bentheogennema*. Since 1961, studies of the fauna and ecology of the mesopelagic waters off the coast of Oregon have been conducted by members of the School of Oceanography, Oregon State University. Several unusual species of macrurous decapod Crustacea have been obtained. The discovery and identification of this new species of *Bentheogennema* was by Carl Forss, who entrusted his material to the authors. Subsequent sampling with mid-water trawls has provided detailed information on the distribution and biologyof this shrimp, as well as abundant material for taxonomic description.

METHODS AND MATERIALS

Material for the zoogeographic distribution was collected in Isaacs-Kidd Mid-water Trawls (IKMT) from the research vessels *Yaquina*, *Endeavor*, *John R. Manning*, and *Hugh M. Smith* in the northeastern Pacific, normally within 320 m of the surface (Wasmer 1972). Information on vertical distribution, reproductive biology, and growth of this species was obtained from samples taken on five cruises aboard RV *Yaquina* at a single sampling station 65 nautical miles (120 km) off the central Oregon coast (NH 65–lat. 44°35′N, long. 125°25′W) in 1972-73. Samples at this station were taken both day and night, using an 8-foot IKMT with a five net opening-closing cod end section similar to the one described by Pearcy and Mesecar (1971).

All samples were preserved at sea in 10% buffered Formalin.[4] The samples were later sorted, identified, sexed when possible, and measured. Carapace length (measured from the postorbital margin to the median posterior edge of the carapace) was used as an indication of size. All figures were drawn with the aid of a camera lucida.

In males, sexual maturity was based on three characteristics: 1) petasmata joined; 2) well-developed accessory lobe on anterior surface of the petasma; 3) and dilated vas deferens with large terminal ampoule (indicative of developed spermatophore) at the base of the fifth pereiopod. The combined characteristics of fully developed thelycum and the posterior lateral lobe of the ovary swollen with eggs at the base of the fifth pereiopod were used as signs of sexual maturity in females. Estimates of growth are presented from analysis of length-frequency data.

Section Penaeidea
Family Penaeidae Bate
Subfamily Aristaeinae Alcock
Series Benthesicymae Bouvier
Bentheogennema burkenroadi n. sp.

Types.–Holotype (USNM 150835), male, carapace length (c.l.) 18 mm, from Station lat.

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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51°26′N and long. 138°28′W, Mid-water Trawl No. 857 (MT 857); Allotype (USNM 150836), female, 14.5 mm c.l., station Newport Hydrographic Line 65 nautical miles (120 km) offshore (NH 65), MT 2130; Paratypes: 1 male (USNM 150837), 15 mm c.l., from NH 265, MT604; 2 males (USNM 150838), 8 and 6.5 mm c.l., NH 65, MT 2088; 1 male (USNM 150839), 14 mm c.l., NH 65, MT 2131; 1 male (USNM 150840), 13.5 mm c.l., NH 65, MT 2130; 4 females (USNM 150841), 14.5, 14, 10, 18 mm c.l., NH 65, MT 2130; 4 males (USNM 150842), 12.5 13.0, 13.2, 17.5 mm c.l., NH 65, MT 2130; 1 male (USNM 150843), 9.0 mm c.l., NH 50, MT 570; 1 male (USNM 150844), 9.5 mm c.l., lat. 40°28′, long. 133°46′, MT 613; 3 females (USNM 150845), 13.3, 14.0, 15 mm c.l., NH 65, MT 2121 Net #5; 1 female (USNM 150846), 20.0 mm c.l., NH 65, MT 2133 Net #1; 2 females (USNM 150847), 7 and 10 mm c.l., NH 65, MT 2070 Net #5; 2 males, 1 female (BMNH 1975:10), 14.2, 16.4, 13.2 mm c.l., NH 65, MT 2175 Net #5; 1 female (BMNH 1975:10), 15.7 mm c.l., NH 65, MT 2178 Net #4; 1 female (BMNH 1975:10), 12.6 mm c.l., NH 65, MT 2302 Net #4; 1 male (BMNH 1975:10), 11.5 mm c.l., NH 65, MT 2301 Net #1. Other, nonparatype, material deposited at Los Angeles County Museum; Fisheries Research Board of Canada Biological Station, Nanaimo, British Columbia; and School of Oceanography, Oregon State University, Corvallis, Oreg.

Diagnosis.—Benthesicymae with podobranch on second maxilliped to third pereiopod inclusive; first maxilliped with single rudimentary arthrobranch; only sixth abdominal somite with middorsal carina; telson distally truncate, usually with single pair of mobile terminal lateral spinules. Accessory lobe of petasma characterized by large upturned terminal hook. Plate of thelycum on sixth thoracic sternite triangular and elevated, projecting ventrally in strong ridge; plate on eighth thoracic sternite pentagonal with anteriormost angle concave and anterolateral margins bearing spines.

Description.—Rostrum extending to level of eye tubercle, well elevated above middorsal carina of carapace (Figure 1). Margin between rostral tip (apex) and dorsal spine with usual setal fringe (although broken in type). Middorsal carina of carapace bearing minute tubercle posterior to

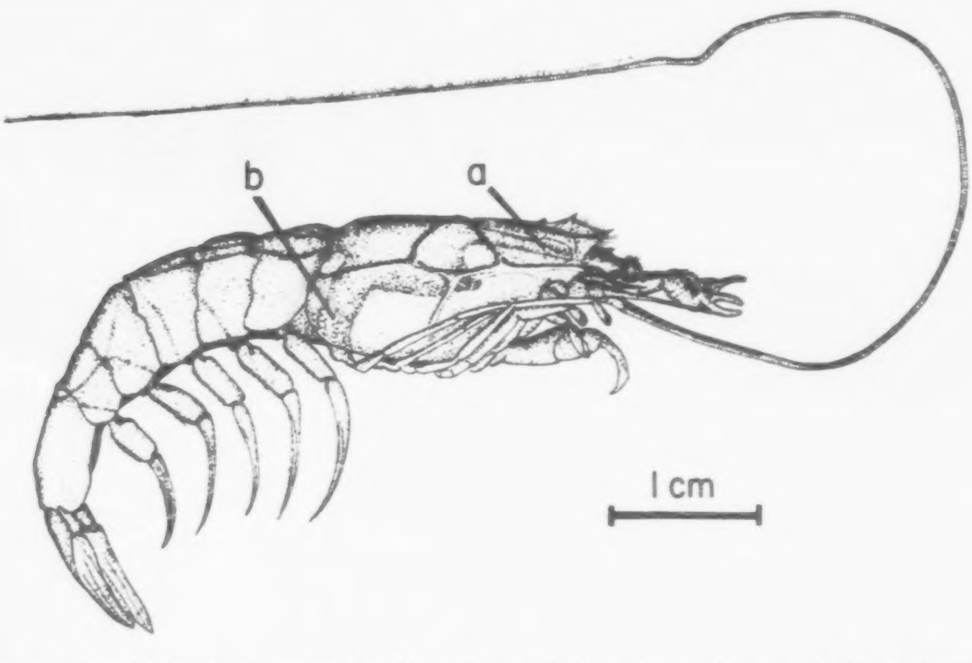

FIGURE 1.—Mature female *Bentheogennema burkenroadi* n. sp. illustrating the (a) anterior and (b) posterolateral lobes of the ovary.

dorsal spine; carina absent between well-defined cervical and postercervical sulci and on posteriormost portion of the carapace. Mid-lateral longitudinal carina consisting of strong antennal carina continuous with hepatic and branchial carinae. Branchiostegal spine small and branchiostegal carina distinct; hepatic sulci continuous from branchiostegal spine towards lower margin of carapace; post-hepatic carina orientated dorsoventrally from longitudinal hepatic carina toward inferior margin of carapace. Antennal angle obtuse and infra-antennal angle acute (Figure 2a).

Only sixth abdominal somite with middorsal carina; second through fifth abdominal somites with weak lateral ridges in approximately dorsoventral position extending from mid-lateral to ventrolateral edge of the pleuron. Fourth, fifth, and sixth abdominal somites with prominent, roughly transversal, lateral ridges which together form "half moon" area (Figure 1). Fourth and fifth abdominal somites bearing small mid-lateral tooth on posterior margins.

Antennal flagellum (Figure 1) similar to *Gennadas* (Foxton 1969), having proximal and distal sections divided by short series of annuli forming kink in flagellum; proximal section rigid, bearing scattered short nonplumose setae; distal section bearing paired arched plumose setae with small plumose setae perpendicular to flagellum at irregular intervals between bases of some arched pairs. Second element of antennular peduncle, along dorsal midline, 0.7 ultimate element (Figure 2b). Antennal scale (Figure 2c) little less than 3 times as long as greatest width; distinct spine (outer margin of scale), slightly convex, terminal end free, not extending beyond narrow apex of blade.

Mandible (Figure 2d) with two segmented palp; palp thickly covered with setae on medial and lateral margins, distal element not quite as long as widest portion of basal element. Endopod of first maxilla (Figure 2e) distally narrow, with tip rounded; proximal gnathobasic lacinia (endite of coxa) subequal in width to distal lacinia (endite of basis), both terminating in strong spines among setae fringe. Anterior lobe of proximal lacinia (endite of coxa) of second maxilla (Figure 2f) strongly constricted behind apex, not broader than posterior lobe of distal lacinia (endite of basis); anterior lobe of distal lacinia very broad; endopod distally long and narrow, with two (sometimes three) curved spines at base of apical portion.

Endopod of first maxilliped (Figure 2g) reaching beyond endite of basis but falling short of exopod; endopod of four elements, third less than twice second; fourth extremely minute; first element bearing usual compliment of three curved spines on distomesial margin. Exopod bladelike, without constricted, segmented distal portion. Merus of second maxilliped (Figure 2h), including anterior prolongation, 1.9 times as long as wide; dactylus with single strong apical spine surrounded by medium and small spines back to proximal end of propodus; merus and carpus with numerous spines and setae; podobranch present. Third maxilliped (Figure 2i) reaching to, or beyond, middle of ultimate joint of antennal peduncle; ischium nearly 3 times as long as greatest width; merus usually twice as long as greatest width; carpus slightly longer than propodus; dactylus with long slender terminal spine; podobranch present.

Merus of first pereiopod (Figure 3a) 1.4 times length of carpus and 1.7 ischium; fingers slightly setose. In second pereiopod (Figure 3b), carpus 1.2 times length of propodus; merus 1.2 carpus and 1.5 propodus; chela with heavy tufts of bristles. Merus and carpus of third pereiopod (Figure 3c) of equal length, each twice ischium; fingers of chela similar to those of second pereiopod. Carpus and propodus of fourth pereiopod nearly equal, each approximating two-thirds of merus which is 2.4 times ischium. Propodus of fifth pereiopod subequal to carpus which is subequal to merus; ischium slightly more than one-third of merus.

Outer scale of appendix masculina (Figure 3d) longer than inner; proximal half of lateral margin expanding slightly then tapering toward base. Inner scale broadly rounded distally; spines on distomesial margin (few to many) long and thin, spines on distal margin smaller, stronger, and of uniform length.

Telson with single pair of mobile terminal-lateral spines (Figure 3e) fringed with setae on terminal and distal two-thirds of lateral margins (of the large number of specimens inspected, only two mature males had any indication of more than one pair of mobile spines (USNM 150839, 150840), each with two pair of mobile spines on terminal edge of telson). No mobile nonterminal-lateral spines present on telson. Lateral margins of lateral rami of uropods (Figure 3f) bearing spine at 0.78 total length. Mesial rami about 0.73 lateral rami.

Each half of petasma (Figure 3g, h), distally divided into three lobes (external, median, and in-

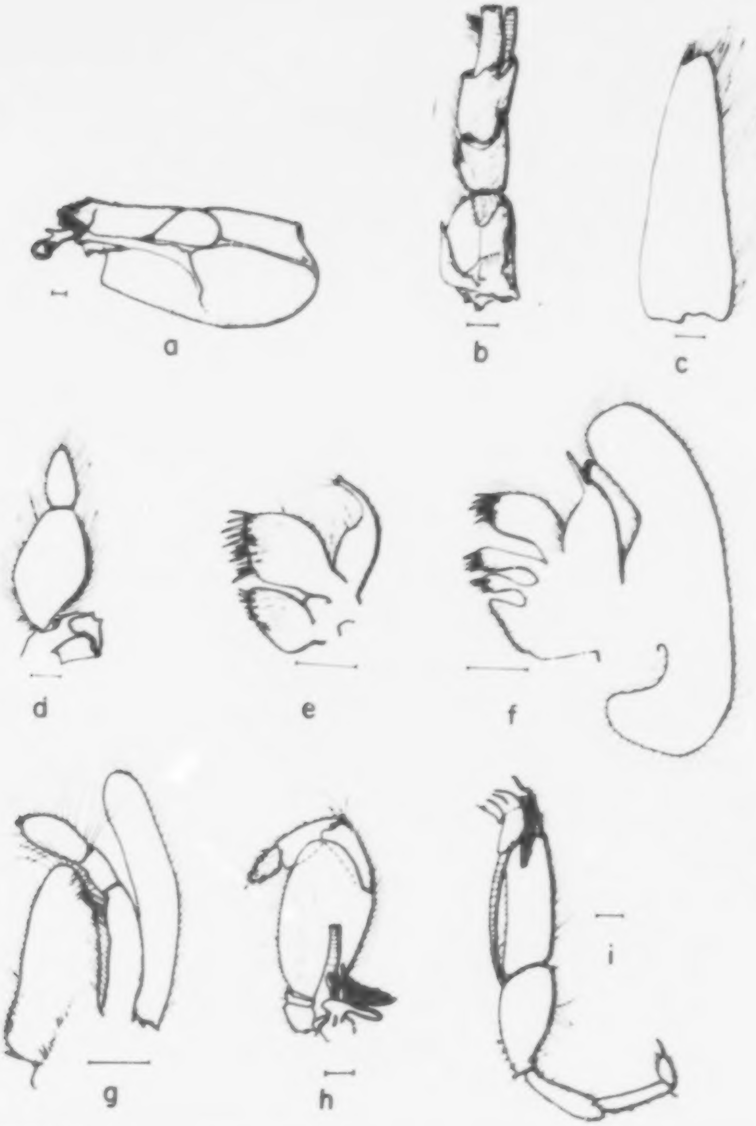

FIGURE 2.—*Benthoogennema burkenroadi* n. sp. (Holotype, male 18 mm carapace length) a, carapace; b, antennular peduncle; c, antennal scale; d, mandible; e, first maxilla; f, second maxilla; g, first maxilliped; h, second maxilliped; i, third maxilliped. Scale equals 1 mm.

ternal (Balss 1927) which are equivalent to Burkenroad's (1936) distoventral, distolateral, and distomedian lobes). External lobe bipartite; lateral part elongate projection with minute terminal teethlike protuberances distally; mesial part curving inward with apex directed toward median lobe. Median lobe broadly rounded; subdistally, accessory lobe on anterior face of petasma, characterized by large upturned terminal hook (Figure 3g) with free margin attaching to base of

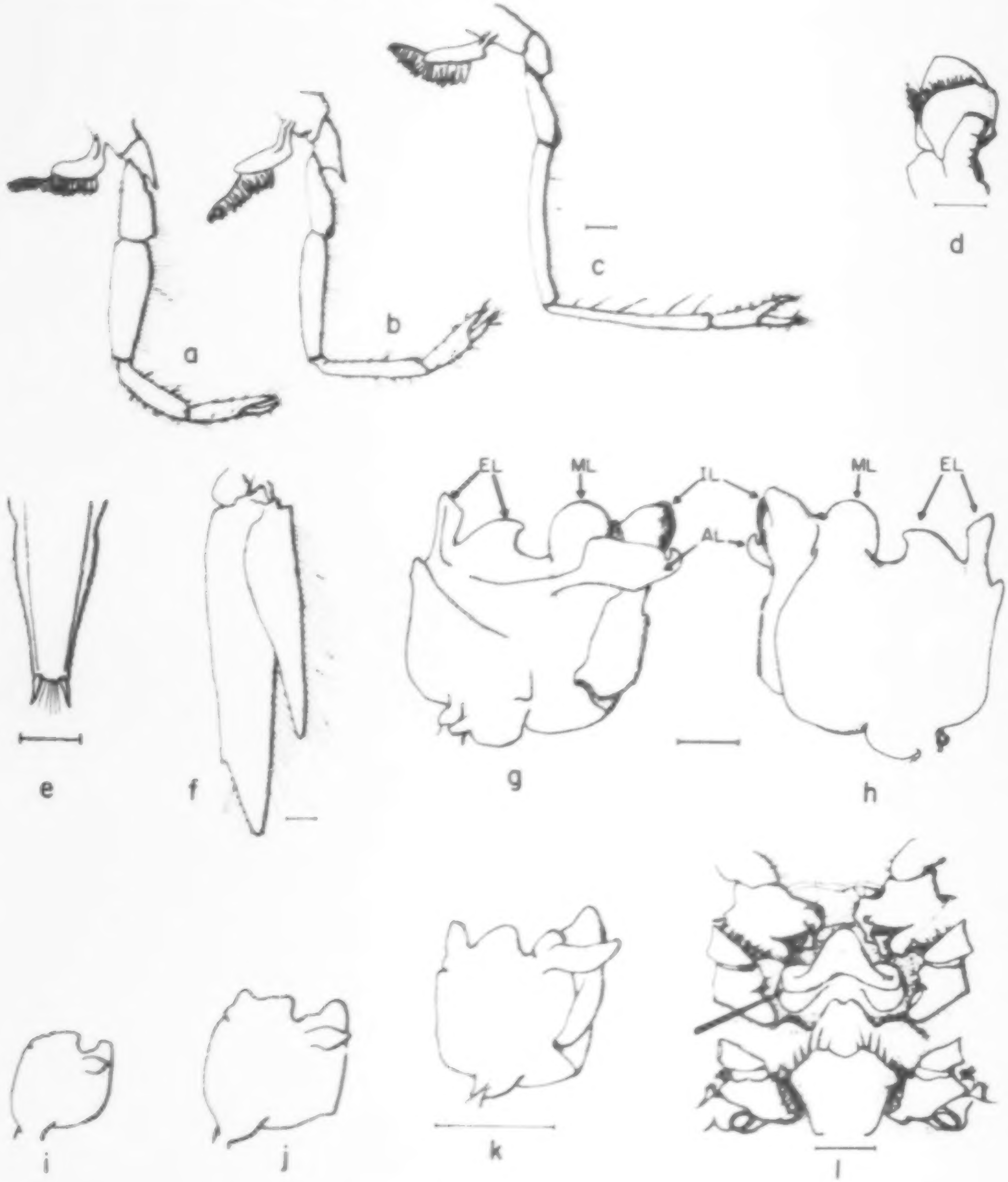

FIGURE 3.–*Bentheogennema burkenroadi* n. sp. (Holotype, male 18 mm carapace length) a, first pereiopod; b, second pereiopod; c, third pereiopod; d, appendix masculina; e, distal half of telson; f, uropod; g, anterior view of petasma (EL = external lobe, ML = median lobe, IL = internal lobe, AL = accessory lobe); h, posterior view of petasma; i, anterior view of petasma from young male (8.0 mm c.l.); j, anterior view of petasma from young male (9.0 mm c.l.); k, anterior view of petasma from young male (9.5 mm c.l.); l, thelycum of female (17 mm c.l.), arrow pointing to right sperm receptacle. Scale equals 1 mm.

median lobe, attachment area distinguishable to level of elongate projection of external lobe. Internal lobe undivided, bearing rigid hooks continuous with row of cincinnuni, holding two halves of petasma together. The accessory lobe develops early in the juvenile stage (Figure 3i, j, k) and together with characteristic spination of telson and presence of podobranchs behind second maxilliped, young of this species were discernable to a size of 6 mm c.l. (the smallest size captured).

Thelycum (Figure 3l) with plate on eighth thoracic sternite pentagonal, with anteriormost angle concave, anterolateral margin bearing long spines (this plate exhibits greatest variation during growth, being more rectangular in young females, changing to the pentagonal shape of maturity but becoming almost bilobed in very large females). Plate of seventh thoracic sternite bearing three anterior directed projections; lateral pair, shortest, bearing short spines; center projection exhibits varying amount of concavity after maturity such that distolateral margins may appear as raised wings. Elevated plate on sixth thoracic sternite triangular and inverted "V" shaped, with apex pointing anteriorly; apex not reaching anterior limit of sternite. Sperm receptacles located toward lateral edges near bases of inverted V.

Coloration at time of capture varying from deep red over entire body to medium red on cephalothorax and lighter on abdomen. Black pigment fleck on distolateral edge of ocular peduncle just below corneal region (Figure 2a). Other small flecks of purple pigmentation often observed on carpus and propodus of third maxilliped and first and second pereiopods, on carpus of third pereiopod, and on ventral surface of abdominal somites just anterior to lateral edge of base of each pleopod.

Remarks.–Burkenroad (1936) proposed the genus *Bentheogennema* for those species of *Gennadas* Bate which possesses podobranchs on the second maxilliped to third pereiopods inclusive. Other generic characters he included were: arthrobranch of first maxilliped large and richly plumose; exopod of first maxilliped without a constricted, segmented distal portion; dorsal carina on sixth abdominal somite only; telson with truncated apex and more than a single pair of mobile lateral spinules.

As is often the case, the addition of a new species changes the generic formula for that group. The new species is similar to *Gennadas* in the armature of the telson but more closely resembles *Bentheogennema* with podobranchs on the second maxilliped through third pereiopod. We agree with Kemp (1909) and Burkenroad (1936) that the presence of podobranchs, a primitive characteristic, is a more important generic trait than the number of pairs of spines on the telson.

We found that the two species of *Bentheogennema*–*B. borealis* (Rathbun) and *B. burkenroadi* n. sp.–from the Oregon coast lack the large, richly plumose arthrobranch on the first maxilliped that Burkenroad (1936) included as a generic characteristic. Both have small rudimentary arthrobranchs similar to *Gennadas*. We assume that Burkenroad (1936) did not have samples of *B. borealis* but included this arthrobranch structure as a generic characteristic from samples of *B. intermedium* (Bate) and *B. pasithea* (Man).

Although Tirmizi (1959) stated that the endopod of the first maxilliped is five-segmented in *Gennadas* and apparently only four-segmented in *Bentheogennema*, we have found that *Gennadas propinquus* Rathbun off the Oregon coast has a four-segmented endopod. Hence these characters are not reliable to distinguish these two genera.

Bentheogennema burkenroadi can be separated from *B. borealis*, *B. intermedium*, *B. pasithea*, and *B. stephenseni* (Burkenroad) by the armature of the telson, and the structures of the petasma and thelycum. The telson of *B. burkenroadi* typically possesses only a single pair of terminal-lateral spines, whereas the other members of this genus possess two or more pairs of lateral spines: *B. borealis* and *B. stephenseni* two pairs; *B. pasithea* three pairs; *B. intermedium* (as described by Tirmizi 1959) four pairs. The number of spines present on the telson should not be held as an invariable characteristic, there is undoubtedly a small percentage of variation as exemplified by the two males of *B. burkenroadi* (USNM 150839, 150840) which possess two pairs of terminal spines. It is possible that one of the two specimens of *Gennadas calmani* (Kemp) (synonymy: *B. borealis*), which Kemp (1909) illustrated with two pairs of terminal spines is also an example of such variation.

The petasma of this new species is unique and easily distinguishable from that of other members of the genus. The combined structures of the accessory lobe with its mode of attachment, its large size, and its terminal hook (present in mature individuals) and the shape of the bipartate external lobes make identification, even of the juvenile stages (Figure 3g-k), possible.

The thelycum differs from that seen in other species by the pentagonal shape of the plate on the eighth thoracic sternite and the elevated triangular plate on the sixth sternite (Figure 3l).

We have named *B. burkenroadi* after Martin D. Burkenroad, whose work on Crustacea, especially the Penaeidae, is well known.

GEOGRAPHICAL AND VERTICAL DISTRIBUTION

Shrimps were examined from mid-water trawl collections taken over much of the North Pacific (Figure 4). *Bentheogennema burkenroadi* was found only in collections from the northeastern sectors (lat. 52-34°N and east of long. 142°W) (Wasmer 1972). Pearcy and Forss (1966, 1969) observed *B. burkenroadi* off the coast of Oregon, as close as 28 km to the northern end of the coast and occurring ≥92 km off the central and south coast. Wasmer (1972) found the greatest concentration in the Transitional Water Mass (Figure 5), with a few individuals occurring in the Pacific Subarctic and eastern North Pacific Central Water Masses. It is assumed to be a transitional species, although as is the case for many shrimps, it is not totally confined to a single physicochemically definited water mass (Wasmer 1972). Since *B. burkenroadi* is a deep mesopelagic species and most of the available geographical collections were from shallow depths, the known geographic range will undoubtedly be increased by more systematic deep trawls in the eastern Pacific.

This species was captured in opening-closing nets from the surface to 1,000-m depth. It apparently demonstrates a diel vertical migration. The depth distribution is, with few exceptions, below 500 m during the day and below 100 m at night (Table 1). Neither day nor night distributions are confined to a narrow depth stratum but are diffused in concentration over a broad range. The nocturnal migration into the upper waters appears to entail only a small segment of the population with the main concentration remaining at depth. Those migrating above 500 m included both sexes, though the immature shrimp (<11-mm

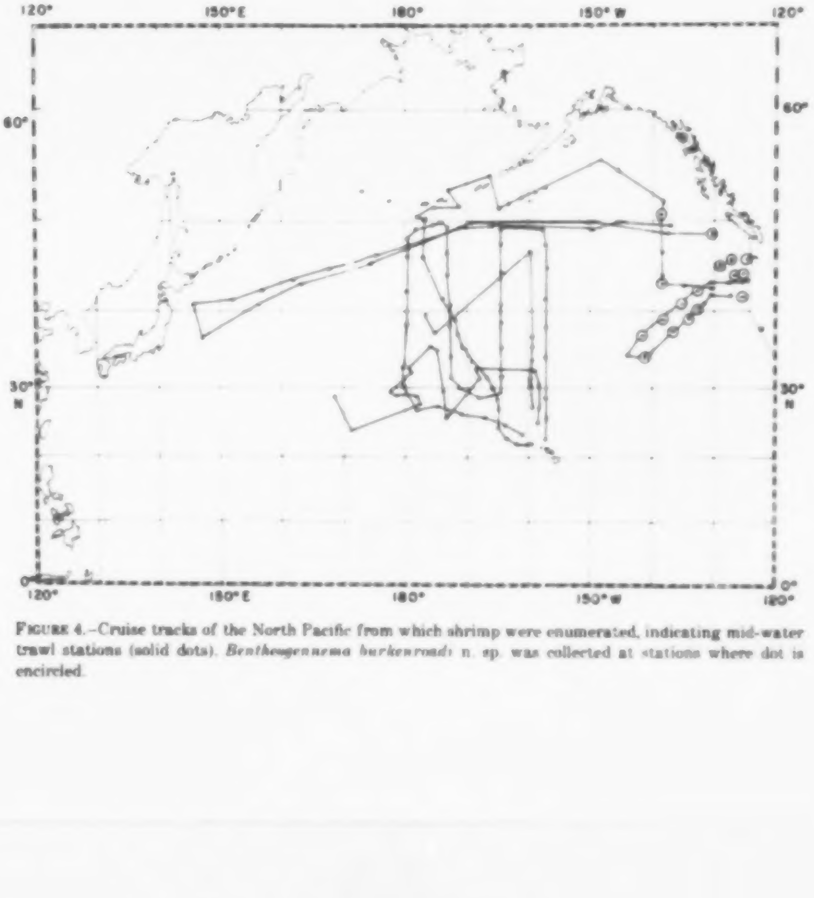

FIGURE 4.—Cruise tracks of the North Pacific from which shrimp were enumerated, indicating mid-water trawl stations (solid dots). *Bentheogennema burkenroadi* n. sp. was collected at stations where dot is encircled.

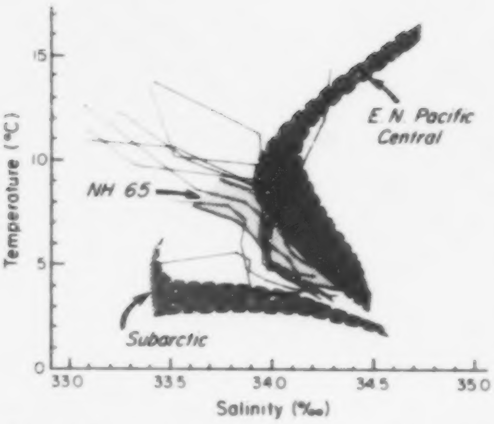

FIGURE 5.—Zoogeographical temperature-salinity (T-S) capture diagram for *Bentheogennema burkenroadi* n. sp. Relevant water masses in darkest bands; medium band in T-S envelope for the station 65 nautical miles off Newport, Oreg. (NH 65); single lines indicate T-S diagram for sampling stations other than NH 65 where this shrimp was captured.

males and <12-mm females) were not observed to migrate as high in the water column as adults. Vinogradov (1968) earlier stated that the intensity of diurnal migration of zooplankters increases with age, and migration may be absent in early stages of development, and our observations concur with this.

More shrimp were caught in nighttime than daytime tows. This may be explained by enhanced visual avoidance of the net during the day (Pearcy and Laurs 1966). However, the lack of obvious differences in size structure between day and night caught shrimp (Figure 6) argues against increased daytime avoidance, as larger more mobile animals should be preferentially sampled at night. Another explanation for the increased nighttime catch, as suggested for *Acanthephyra purpurea* Milne-Edwards and *Gennadas valens* (Smith) by Foxton (1970a, b), is migration up from below our maximum sampling depth of 1,000 m. Such a migration is indicated by the high concentrations between 600 and 1,000 m both day and

TABLE 1.—Seasonal diel vertical distribution to a depth of 1,000 m of mature males (≥11 mm c.l.), mature females (≥12 mm c.l.), and sexually immature male and female *Bentheogennema burkenroadi* at a sampling location 65 nautical miles (120 km) off Newport, Oreg. (lat. 44°35′N - long. 125°30′W).

Time of year	Size group	Depth (m)											
		0-50	50-100	100-150	150-200	200-300	300-400	400-500	500-600	600-700	700-800	800-900	900-1,000
							DAY						
June 1972	Mature males									3	4	2	2
	Mature females									3	2	3	2
	Immatures								1	5	6	2	2
Sept. 1972	Mature males								1	2	6	4	1
	Mature females								2		8	2	4
	Immatures										2	1	1
Nov. 1972	Mature males			1				1	2	2	4	5	
	Mature females				1				2	3	3		1
	Immatures									1	1		1
Mar. 1973	Mature males										[1]3		
	Mature females										[1]1		
	Immatures						1		1		[1]1		
Total number				1	1		1	1	9	19	41	19	14
Total volume in 1,000 m^3		103.5	149.9	103.2	94.7	474.7	497.9	310.9	259.6	132.6	182.3	183.3	162.4
Number/1,000 m^3 (day)		0	0	0.0097	0.0106	0	0.0020	0.0032	0.0347	0.1433	0.2240	0.1037	0.0862
							NIGHT						
June 1972	Mature males	1				1	3				1		
	Mature females						1	3		1			
	Immatures						2	2					
Sept. 1972	Mature males	[2]2			1	1	1	4	5	[2]1	2	1	1
	Mature females			1	2		5	2	2		3	1	4
	Immatures						3	1	1	1	5		
Nov. 1972	Mature males					1	5	2		7	3		6
	Mature females				[2]1	4	7	2	1	5	1	1	4
	Immatures					1		1		1	3		1
Mar. 1973	Mature males				3	3	1	1	1	1	1		
	Mature females			1	1	4	2	1	1	2			
	Immatures					2			1	1			
Total number		3		2	8	17	30	19	12	20	19	3	15
Total volume in 1,000 m^3		111.8	530.6	184.8	292.8	251.0	435.9	288.6	261.6	147.2	170.7	132.3	129.3
Number/1,000 m^3 (night)		0.0268	0	0.0108	0.0273	0.0677	0.0688	0.0658	0.0459	0.1359	0.1113	0.0227	0.1160

[1] Twilight 1 h after sunset.
[2] Twilight 1 h before sunrise.

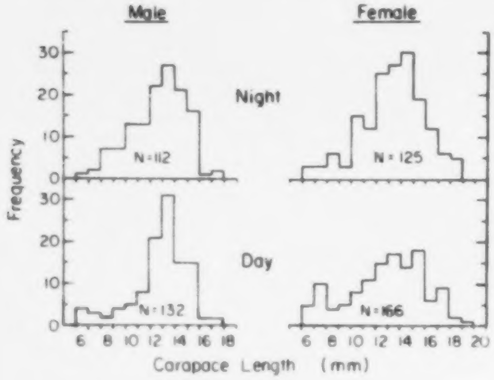

FIGURE 6.—Day and night length-frequency distributions of male and female *Bentheogennema burkenroadi* n. sp.

night with no progressive drop in concentration with increased depth to 1,000 m (Table 1).

The slight upward movement of this species may be related to its morphology. Vinogradov (1968) considers reduced musculature and a thin integument, which we observed in *Bentheogennema burkenroadi*, to be a means of achieving buoyancy. Because of weak swimming musculature, they may swim too slowly to keep pace with the upward movement of the stimulating isolume, resulting in broad day and night distributions (Donaldson 1973).

REPRODUCTION

Since penaeid shrimp do not brood their eggs, a description of the breeding cycle must rely on anatomical changes, especially in the development of the ovary and ova. The female reproductive system consists of a bilaterally symmetrical ovary and paired oviducts internally, and externally of a thelycum. Each half of the mature ovary has an anterior lobe angling from the cervical sulcus and almost reaching the base of the eye, and then folding back along itself (Figure 1a). The anterolateral lobe lies over the hepatopancreas extending approximately one-half the way down the body wall. The posterolateral lobe, of such a mature ovary, will have visible distinct ova, measuring up to 240-288 μm crossectional diameter, and will extend ventrally, making a pouchlike structure at the base of each of the fifth pereiopods (Figure 1b). The posterior lobes extend beneath the dorsal abdominal muscle bands, becoming swollen in the first abdominal segment and then extending on toward the end of the third segment. Females were considered to have reached maturity after attaining a size of 12 mm c.l. and males at a size of 11 mm c.l.

The reproductive cycle, as judged from the sexual condition of the testis and ovary, appears to consist of a 4- to 6-mo spawning season and a 6- to 8-mo resting phase. Based on samples collected in 1972 and 1973, the carapace of females in June is fairly rigid, though the ovaries are not ripe. Some males, from external observation, appear to be ready to release sperm, though most display only partial swelling of the terminal ampoule and vas deferens or lack swelling at all. By fall, females exhibit developing ovaries (two females were in spawning condition), and the carapace is correspondingly rigid. Most males have full, ripe looking testes and dilated terminal ampoules. By the end of November, spawning is in evidence. Most females are mature with readily distinct ova; some mature females have evidently spawned as the thoracic cavity appears empty; the carapace is correspondingly nonrigid, due to the spent ovary which had crowded much of the other organs; others have developing ovaries distended by small diameter ova. All males at this time have ripe testes and dilated terminal ampoules. By February, 50% of all females exhibit signs of spawning activity; the rest have probably spawned because their thoracic cavities appear empty and the carapace nonrigid due to the flaccid ovary. Most males still exhibit ripe testes and enlarged terminal ampoules.

The sex ratio for adult males to females (N = 440), when all tows are included, was: 1:1, 1:1.08, 1:1, 1:1.02, and 1.03:1 for the respective cruises. This approximate 1:1 sex ratio, if it applies to all ages, indicates that there is no selective mortality by sex for this species (Geise 1959).

GROWTH

If spawning occurs from November through February and young (6-7 mm c.l.) enter the population April through June (Figure 7), the intervening egg and larval stages must take 3 to 5 mo. Based on size frequency diagnosis, about 12 additional months are required to reach maturity (11-12 mm c.l.) and another 5 to 6 mo are required before spawning commences Thus the generation time is estimated to be about 2 yr. The largest

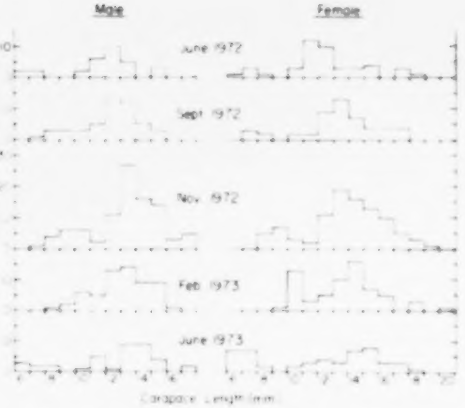

FIGURE 7.–Length-frequency histograms of *Bentheogennema burkenroadi* n. sp., from the five cruises (1972-73) off the Oregon coast.

shrimp captured were a 17-mm c.l. male and a 20-mm c.l. female.

Since the mesh size of the net liner was small enough to retain the young (6-7 mm c.l.) and we assume equal chance of capture of young and adults, then adults apparently live more than a year or two after first spawning because the number of adults captured is greater than the number of immature. In fact, the 12- to 15-mm mode must consist of greater than one age class since by itself it exceeds the juveniles in number. This overlap of age classes at >12 mm c.l. indicates that growth slows after maturity is reached.

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LITERATURE CITED

BALSS, H.

1927. Macrura der Deutschen Tiefsee-Expedition. 3. Natantia, Teil B. Wiss. Ergeb. dtsch. Tiefsee-Exped. "Valdivia" 23(6):247-275.

BURKENROAD, M. D.

1936. The Aristaeinae, Solenocerinae and pelagic Penaeinae of the Bingham Oceanographic Collection. Materials for a revision of the oceanic Penaeidae. Bull. Bingham Oceanogr. Collect., Yale Univ. 5(2), 151 p.

1940. Preliminary descriptions of twenty-one new species of pelagic Penaeidea (Crustacea Decapoda) from the Danish Oceanographical Expeditions. Ann. Mag. Nat. Hist., Ser. 11, 6:35-54.

DONALDSON, H. A.

1973. The ecology of the genus *Sergestes* (Decapoda, Natantia) in an area near Bermuda. Ph.D. Thesis, Univ. Rhode Island, Kingston, 234 p.

FOXTON, P.

1969. The morphology of the antennal flagellum of certain of the Penaeidea (Decapoda, Natantia). Crustaceana 16:33-42.

1970a. The vertical distribution of pelagic decapods [Crustacea: Natantia] collected on the Sond Cruise 1965. I. The Caridea. J. Mar. Biol. Assoc. U.K. 50:939-960.

1970b. The vertical distribution of pelagic decapods [Crustacea: Natantia] collected on the Sond Cruise 1965. II. The Penaeidea and general discussion. J. Mar. Biol. Assoc. U.K. 50:961-1000.

GIESE, A. C.

1959. Comparative physiology: Annual reproductive cycles of marine invertebrates. Ann. Rev. Physiol. 21:547-576.

KEMP, S.

1909. The decapods of the genus *Gennadas* collected by H.M.S. 'Challenger.' Proc. Zool. Soc. Lond. 1909:718-730.

MAN, J. D. DE.

1911. The Decapoda of the Siboga Expedition. Part I. Family Penaeidae. Siboga Exped. Monogr. 39a, 131 p.

PEARCY, W. G., AND C. A. FORSS.

1966. Depth distribution of oceanic shrimps (Decapoda; Natantia) off Oregon. J. Fish. Res. Board Can. 23:1135-1143.

1969. The oceanic shrimp *Sergestes similis* off the Oregon coast. Limnol. Oceanogr. 14:755-765.

PEARCY, W. G., AND R. M. LAURS.

1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

PEARCY, W. G., AND R. S. MESECAR.

1971. Scattering layers and vertical distribution of oceanic animals off Oregon. *In* G. B. Farquhar (editor), Proc. Int. Symp. Biol. Sound Scattering Ocean, p. 381-394. Ocean Sci. Program, Mar. Cent. Ocean Sci., Dep. Navy, Wash., D.C.

RATHBUN, M. J.

1902. Descriptions of new decapod crustaceans from the west coast of North America. Proc. U.S. Natl. Mus. 24:885-905.

TIRMIZI, N. M.

1959. Crustacea: Penaeidae. Part II. Series Benthesicymae. The John Murray Expedition 1933-1934 Sci. Rep. 10(7):319-383.

VINOGRADOV, M. E.

1968. Vertical distribution of the oceanic zooplankton. A.N. SSSR Inst. Okeanol. (Translated from Russian, Israel Program Sci. Transl., 1970, 338 p., Natl. Sci. Found. TT 69-59015.)

WASMER, R. A.

1972. Zoogeography of pelagic shrimps (Natantia: Penaeidea and Caridea) in the North Pacific Ocean. Ph.D. Thesis, Oregon State Univ., Corvallis, 232 p.

THE AMERICAN SAMOA LONGLINE FISHERY, 1966-71

HOWARD O. YOSHIDA[1]

ABSTRACT

Aspects of the longline fishery based at American Samoa covering the period from 1966 to 1971 are described. The fishery is discussed primarily as it relates to the albacore, *Thunnus alalunga*, and to a small extent the yellowfin tuna, *T. albacares*. The landings of albacore fluctuated between 17,722 and 28,310 metric tons from 1966 to 1971. Although no downward trend was evident in the relation between total landings and total effort, the relation between CPUE (catch per unit of effort) and effort showed a definite downward trend. Generally, fishing effort was confined to the north of lat. 20°S in the first and fourth quarters. In the second and third quarters large amounts of effort were also expended south of lat. 20°S. The length-frequency distribution of albacore showed that albacore sizes were stratified by latitude. North of lat. 20°S the size of albacore was rather uniform, in that only a single mode was evident in the length-frequency distributions. South of lat. 20°S two or more modes were evident.

The Honolulu Laboratory of NMFS (National Marine Fisheries Service) has been involved in assessing and monitoring the fisheries resources and developing the high seas fishing industry of the territories and island possessions of the United States in the Pacific Ocean. Part of this work included an investigation of the longline fishery based in American Samoa, which resulted in a report describing the history of the fishery and the distribution, apparent abundance, and size composition of albacore, *Thunnus alalunga*, landed from 1954 to 1965 (Otsu and Sumida 1968). The present report describes the status of the American Samoa longline fishery from 1966 to 1971; it is timely because the fishery has changed considerably since 1965, particularly with regard to the apparent abundance of albacore. Data published by Otsu and Sumida will also be used, especially where they are useful in illustrating certain continuing trends.

The earlier report included a rationale for confining the study to the albacore, the principal species of tuna taken in the fishery. The data were reliable only with respect to albacore because the catches of the other species were often not sold in their entirety to the canneries and, therefore, were not included in the catch reports by the vessel operators. However, as will be discussed later, the vessel operators have expended a considerable amount of effort to catch yellowfin tuna, *T. albacares*, in recent years. It is believed that most of the yellowfin tuna are now included in the catch reports and this species has become an important factor in the American Samoa longline fishery, and can no longer be ignored.

The tuna canneries, operated by Star-Kist Samoa, Inc. and the Van Camp Sea Food Company, depend entirely upon deliveries made by foreign flag vessels and fishermen. One of the most notable changes in the fishery over the years has been in terms of vessel nationality. The fishery began in 1954 with seven Japanese vessels. Vessels from Korea entered the fishery in 1958, and from the Republic of China (Taiwan) in 1964. The Japanese continued to increase their participation until 1963, but thereafter began a gradual withdrawal. On the other hand, the vessels from Korea and Taiwan greatly increased in number until the fleet reached a peak in 1967. Due largely to the withdrawal of the Japanese, the fleet has decreased since 1967. During the last quarter of 1971 there were 209 vessels in the fleet, consisting of 4 from Japan, 90 from Korea, and 115 from Taiwan.

SOURCES OF DATA

The data in this report were obtained through the operation of a field station in American Samoa, established in 1963, and manned continuously through December 1970 by personnel from NMFS, Honolulu. In January 1971 the field station was taken over by the Office of Marine Resources, Government of American Samoa. In the begining, the length, weight, and sex of 50 albacore, randomly chosen, were obtained from each trip landing. For various reasons, e.g.,

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changes in cannery operating procedures, changes in the sampling procedures were necessitated in subsequent years. The collection of sex and weight data was discontinued in early 1971. Catch and effort data have been provided voluntarily by the fishing vessel operators from about 75% of the fishing trips.

The longliners on some occasions fish widely scattered areas on a single fishing voyage. Since there is no way to determine the origin of each fish in the catch and because the fish are sampled at random at the docks, it is probable that some samples included fish from several different locations. This problem was minimized by summarizing the length data by large geographical areas.

ANNUAL LANDINGS OF ALBACORE AND YELLOWFIN TUNA

Except for dips in 1961 and 1964, the albacore landings increased steadily from 1954 to 1965 (Otsu and Sumida 1968). In the 6 yr that followed, the landings fluctuated between 17,722 and 28,310 metric tons (Table 1).

The gain in importance of yellowfin tuna can be seen in the increased landings in the later years (Table 1). After a period (1954 to 1964) of reported landings of less than 2,500 metric tons, the reported landings increased substantially and fluctuated between 4,514 and 8,567 metric tons from 1965 to 1971.

APPARENT ABUNDANCE OF ALBACORE AND YELLOWFIN TUNA

Otsu and Sumida (1968) used various indices of apparent abundance in discussing the status of the fishery for albacore during 1954 to 1965. These indices included catch per trip, catch per day, and catch per 100 hooks. However, because data on number of hooks fished per day were not available for the entire period of their study, they elected to use the fishing trip as the basic measure of effort in analyzing the apparent abundance of albacore. They also examined the relation between catch and effort, and CPUE (catch per unit of effort) and effort, in evaluating the effect of fishing on the stock.

Ideally, in considering the mean annual CPUE as an index of apparent abundance, the fishery should affect all portions of the stock(s) under consideration equally throughout the years. However, since the geographical limits of the fishery have been expanding each year, the situation is almost certainly not ideal. In this section I will extend some of the analyses of Otsu and Sumida to determine if any changes have occurred in the apparent abundance of albacore from 1966 to 1971. Since there are now 9 yr of effort data in terms of the number of hooks fished, I will make greater use of the catch per 100 hooks to determine the apparent abundance of albacore. It is assumed that fishing efficiency is not influenced by the nationality of the vessels, for Skillman (1975) found no evidence to suggest that any gear modification or change in the nationality of the fleet has caused any change in the catchability coefficient of albacore in the Samoan fishery.

TABLE 1.—Total annual albacore and yellowfin tuna landings in American Samoa, 1954-71.

Year	Landings (metric tons)	
	Albacore	Yellowfin tuna
1954	338	597
1955	1,760	1,628
1956	3,680	2,113
1957	5,873	1,537
1958	9,869	2,458
1959	10,292	1,780
1960	10,852	1,134
1961	9,740	1,331
1962	13,326	1,406
1963	13,972	2,057
1964	10,652	2,452
1965	15,591	4,514
1966	25,278	6,531
1967	28,310	5,326
1968	17,722	7,337
1969	18,767	8,207
1970	23,875	7,689
1971	22,193	8,567

Apparent Abundance of Albacore

Otsu and Sumida (1968) analyzed the mean annual CPUE of albacore from 1954 to 1965 in terms of the catch per trip. They believed that the catch per trip was a satisfactory measure of apparent abundance because their analysis showed a close relationship between the monthly average catch per trip and the monthly average catch per day. However, there are some basic shortcomings in the catch per trip. One is that the catch per trip of any vessel is limited by its fish-holding capacity. Also, as indicated by Otsu and Sumida (1968), the catch per trip is influenced by changes in the number of days fished per trip and by changes in the size composition of the vessels in the fleet. Changes in the number of hooks fished per day can also affect the catch per trip. The data do indeed show that the mean number of days fished per trip has increased during recent years (Table 2). The increase in the mean number of days fished per trip may also, in part, indicate change in the size of the vessels. That is, larger vessels, which presumably have larger fish-holding capacities, probably fish more days to obtain a full load of fish.

TABLE 2.–Total trip length, days spent fishing, and traveling time per trip by longline vessels based at American Samoa.

Year	Mean number of days Total trip length	Mean number of days Fishing time per trip	Mean number of days Traveling time per trip
1963	42.35	26.12	16.23
1964	41.26	27.39	13.87
1965	48.79	32.09	16.60
1966	50.58	33.74	17.05
1967	62.13	38.03	23.50
1968	68.02	43.20	24.82
1969	67.34	44.25	23.08
1970	70.74	45.03	25.72
1971	84.16	52.03	32.13

In their analysis of the apparent abundance of albacore from 1954 to 1965, Otsu and Sumida (1968) indicated that the mean catch per trip increased from 1954 through 1960 and then fell slightly and stabilized at a lower level in 1963-64. A continuation of this analysis (Figure 1) showed that the mean catch per trip continued to fluctuate around this lower level with no definite upward or downward trend. It is possible that the mean catch per trip is fluctuating near the mean fish-holding capacity of the vessels or near a level that is related to the profitability of the fishing trip. That is, a vessel may fish as many days as are needed to obtain a full load or until a catch that is at least profitable is obtained. The trip, as an index of effort, does not take this factor into consideration, and, therefore, the catch per trip is not an accurate indicator of the apparent abundance.

It would be useful then, to compare the catch per trip with the catch per day, which is not affected by as many variables as the catch per trip. The mean annual catch per trip from 1959 to 1971 fluctuated between 29.9 and 38.2 metric tons (Figure 2) and, as noted earlier, did not reveal any obvious trends. The mean annual catch per day during the same period fluctuated between 0.7 and 1.7 metric tons, and, contrary to the catch per trip, declined after 1962 suggesting that the longline vessels are fishing more days to compensate for the reduced catch per day. The mean total length of a fishing trip, number of days spent fishing, and number of days spent traveling on each trip (Table 2) all showed an increasing trend from 1963 to 1971, which indicates that, in general, the vessels are traveling farther away from the home base to fish and are fishing more days per trip.

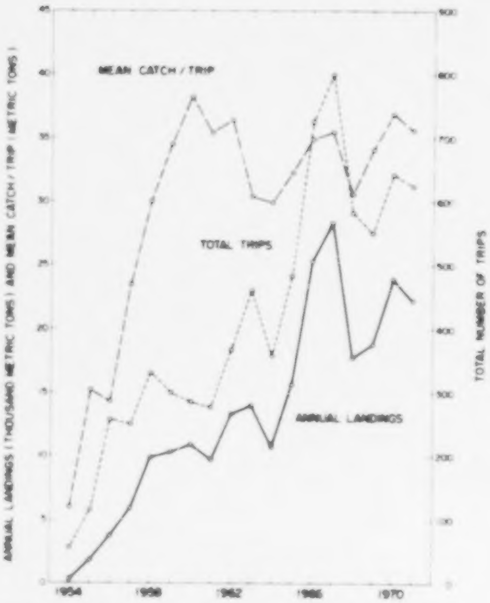

FIGURE 1.–Total number of fishing trips, mean catch of albacore per trip, and annual albacore landings, 1954-71.

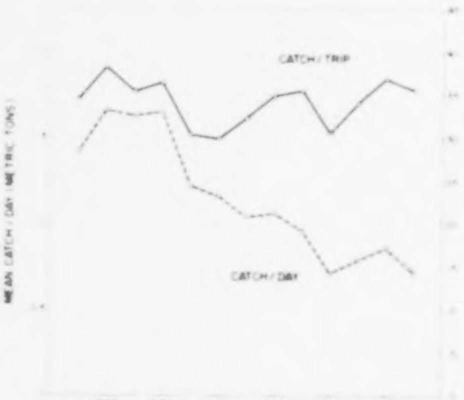

FIGURE 2.–Comparison of the mean catch per day and mean catch per trip of albacore, 1959-71.

The relation between the annual total landings of albacore and the total fishing effort (number of fishing trips) indicated that the annual landings increased with increasing fishing effort from 1954 to 1965. Based on this analysis, Otsu and Sumida (1968) concluded that the point of maximum yield of albacore had not been reached in the American Samoa-based fishery. The fishing effort continued to increase subsequent to 1965, and reached a peak of close to 800 fishing trips in 1967. The albacore landings also continued to increase with the increased effort. The relation between the annual landings and the effort, in total number of days fished, from 1959 to 1967 also showed that the landings increased with increasing fishing effort (Figure 3). The mean catch per day plotted against effort in total number of days fished, however, shows a decline in the CPUE from 1959 to 1971 with increasing effort (Figure 4).

As noted earlier, our laboratory has been obtaining, from the vessel operators, effort data in terms of number of hooks fished since 1963. Using these data, the mean monthly catch per 100 hooks of albacore from 1963 to 1971 was computed (Figure 5). A salient feature of Figure 5 is that the mean monthly CPUE fluctuated much more from 1966 to 1971 than they did from 1963 to 1965. It is not clear what caused this change in trends in the monthly CPUE after 1965. One possibility is that it is related to a geographical change in fishing effort. As will be discussed in more detail in another section, in the years after 1965 more fishing effort has been expended in latitudes south of lat. 20°S where good CPUE's of albacore are obtained in the second and third quarters of the year. This fact could also account for the definite peak in abundance of albacore in June or July during 1966 to 1971. It is also evident, however, that there is a slightly declining trend in the CPUE from 1963 to 1971.

A plot of the total annual catch of albacore against the estimated total annual effort in number of hooks fished from 1963 to 1971 is shown in Figure 6. During this period the estimated total effort ranged from about 13,165,000 to 51,092,000 hooks and the annual albacore catch from 10,652 to 28,310 metric tons. With some minor exceptions, there was a strong positive relation between the annual catch and effort for the 1963-71 period. Generally, the catches increased with increased fishing effort. Suda (1971) also found a similar relationship between albacore catch and fishing effort in the South Pacific from 1952 to 1968.

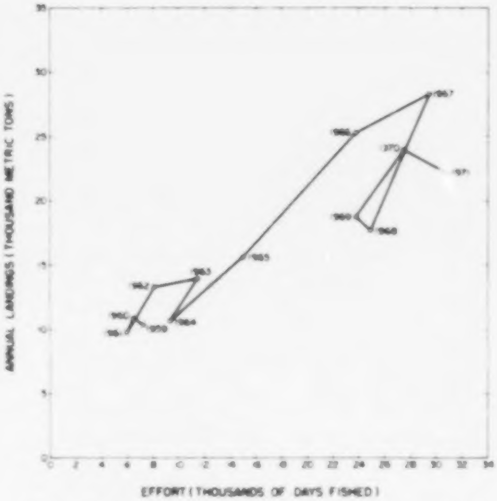

FIGURE 3.—Relation between annual landings of albacore and effort.

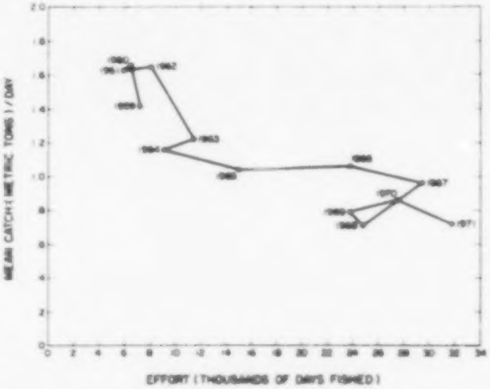

FIGURE 4.—Relation between mean catch of albacore per day and effort.

In Figure 7 is plotted the CPUE in number of fish and in weight per 100 hooks fished against the estimated total annual number of hooks fished from 1963 to 1971. Both plots show a negative relation between CPUE and effort; the CPUE decreased with increased fishing effort. Thus, although the catch has been increasing with increasing effort, it appears that the fishery has had some effect on the stock size in that the CPUE has been declining with increasing effort.

The analyses above reflect average conditions of

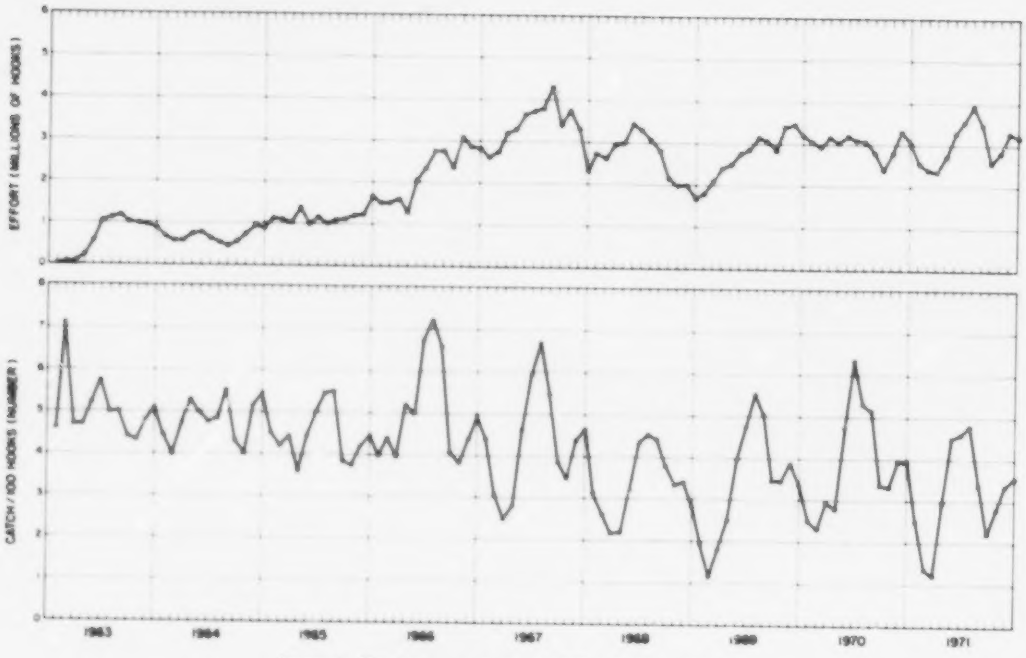

FIGURE 5.–Monthly mean albacore CPUE and effort, 1963-71.

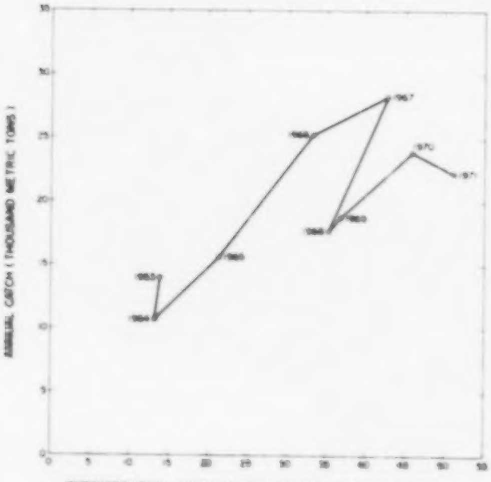

FIGURE 6.–Relation between total catch of albacore and total effort, 1963-71.

the fishery taken as a whole. It is of interest to compare the conditions north and south of lat. 20°S, especially since the geographic boundaries of the fishery have been expanding over the years. That is, it would be useful to see how the CPUE in the older fishing grounds north of lat. 20°S compares with that in the more recently exploited grounds south of lat. 20°S. The annual mean CPUE was computed for the area north of lat. 20°S, which represents the older fishing ground, and the area south of lat. 20°S, which represents the newer grounds (Figure 8). This analysis must be viewed with some caution, however, since total effort expended south of lat. 20°S is less than that expended in the north. Southern waters are fished heavily only in certain quarters of the year and these are the quarters when good catch rates are obtained. The mean catch rates in the southern waters therefore, may be overly weighted by the catch rates obtained in these quarters. However, the mean annual CPUE is higher in the newer grounds than in the old. The mean annual CPUE's

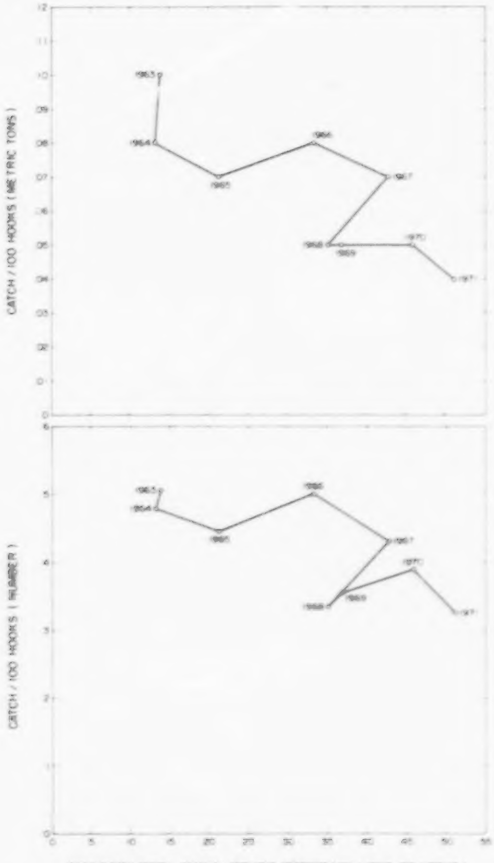

FIGURE 7.—Relation between CPUE of albacore in weight and numbers and total effort, 1963-71.

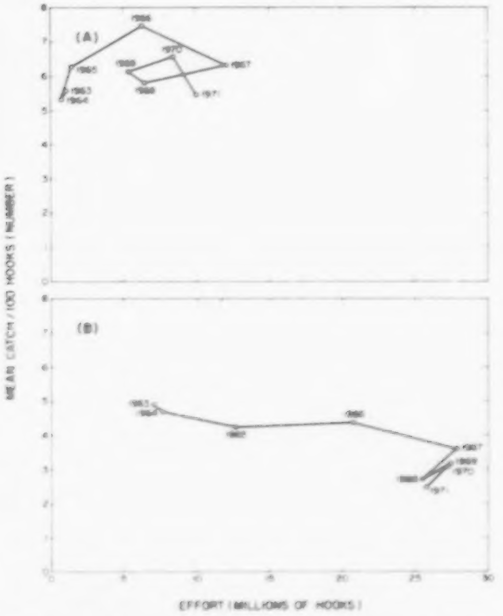

FIGURE 8.—Relation between CPUE of albacore and effort in areas south (A) of lat. 20°S and north (B) of lat. 20°S.

from 1963 to 1971 in the old grounds were all less than five albacore per 100 hooks, whereas in the new grounds they were all greater than five per 100 hooks during the same period. Another difference is that in the old grounds the mean CPUE has been declining with increasing effort. In the new grounds the CPUE increased with increasing effort from 1963 to 1966. In 1967, the CPUE declined slightly and from that year to 1971 the CPUE appears to have stabilized around six albacore per 100 hooks. These facts suggest that the albacore fishery has been able to maintain itself by continuously expanding geographically to take advantage of better CPUE in newer areas. It should be repeated here, however, that despite the expansion into new fishing grounds the overall trend for the fishery has been a decline in CPUE (Figure 5). Furthermore, in the southern grounds to which the fishery has expanded, the albacore catches, as will be shown in a later section, are composed of a large proportion of smaller fish. These smaller albacore may not be the optimum size at which to harvest the stock.

Apparent Abundance of Yellowfin Tuna

The discussion of the apparent abundance of yellowfin tuna will be primarily in terms of how it relates to the apparent abundance of albacore in the Samoan longline fishery. For one thing, although albacore are selectively fished for by the fleet, yellowfin tuna (and small numbers of other species) are also caught by the longlines, and the CPUE for one species may affect the CPUE of another (Rothschild 1967). The CPUE for one species may affect that for another species because, in computing the CPUE, the total effort expended was applied to the catch of each species without regard to the competition of the species for space on the gear. Furthermore, there is another complicating variable: the fishermen apparently seek out yellowfin tuna when the catches of albacore are poor. They do this by modifying the longlines to fish shallower and by fishing closer to the equator where yellowfin tuna catches are known to be better. The fact that the price of yellowfin tuna increased from an average of $270 a ton in 1965 to $394 a ton in 1970 may also have been a factor.

As noted earlier, the CPUE of albacore in relation to increased fishing effort has been declining, especially in the years subsequent to 1967. During 1968 to 1971, the yellowfin tuna CPUE was relatively good. It is apparent that as albacore fishing deteriorated, the vessels expended more effort to catch yellowfin tuna. The relation between albacore and yellowfin tuna CPUE in the Samoan longline fishery from 1963 to 1971 is shown in Figure 9. It appears that an inverse relation existed between albacore and yellowfin tuna CPUE: When yellowfin tuna CPUE was high, albacore CPUE was low, and vice versa. The correlation coefficient (r = -0.6636; df = 7), however, was not significant.

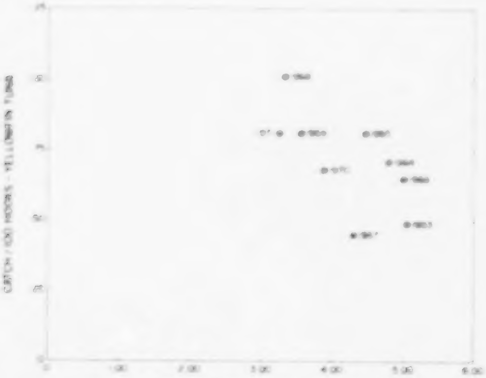

FIGURE 9.–Relation between albacore and yellowfin tuna CPUE.

SPATIAL AND TEMPORAL CONSIDERATIONS

Observations on the American Samoa fishery during the period from 1954 to 1965 indicated that the longline vessels shifted fishing grounds with season (Otsu and Sumida 1968). Seasonal and geographical differences in CPUE, however, were not readily apparent in the early years. In the following sections I will examine the spatial and temporal distribution of effort and CPUE in the fishery from 1966 through 1971.

Effort

In the early years of the fishery, the longliners confined their fishing largely to the vicinity of the Samoa Islands. Over the years, the vessels gradually extended their operations to more distant waters, and by 1965 the fishing grounds reached from about long. 175°E to about long. 120°W between the equator and lat. 30°S (Otsu and Sumida 1968). From 1966 to 1971 there was a further extension of the fishing grounds; the vessels fished from off the east coast of Australia to long. 100°W and from about lat. 10°N to about lat. 40°S. The fishing effort, however, was not uniformly distributed throughout the geographical limits of the fishery. Rather, there were distinct seasonal patterns in the spatial distribution of fishing effort.

A composite geographic distribution of the fishing effort on a quarterly basis for 1966 to 1971 summarized by 2° squares between the equator and lat. 40°S and east of long. 150°E is shown in Figure 10. As composite charts they can reflect only "average" conditions.

In the first and fourth quarters, the vessels generally fished to the north of lat. 20°S, and areas of concentrated fishing effort developed in about the same area each year. In the second and third quarters, the vessels expanded their operations to the south of lat. 20°S and, in addition to the usual area of concentrated effort to the north, an area of high fishing effort also developed to the south of lat. 20°S. However, there apparently has been a change from earlier years in the operations of the fleet because prior to 1966 the vessels fished in the north during both the first and second quarters (Otsu and Sumida 1968). These figures indicate that the vessels are moving south in the second quarter, earlier than previously. In any event, these seasonal changes in the concentration of fishing effort have been interpreted to reflect the movement of albacore in the South Pacific Ocean (Suzuki 1961; Otsu and Sumida 1968).

Catch Per Unit of Effort

The mean quarterly CPUE for 1966-71 plotted by 2° square areas is shown in Figure 11. In a

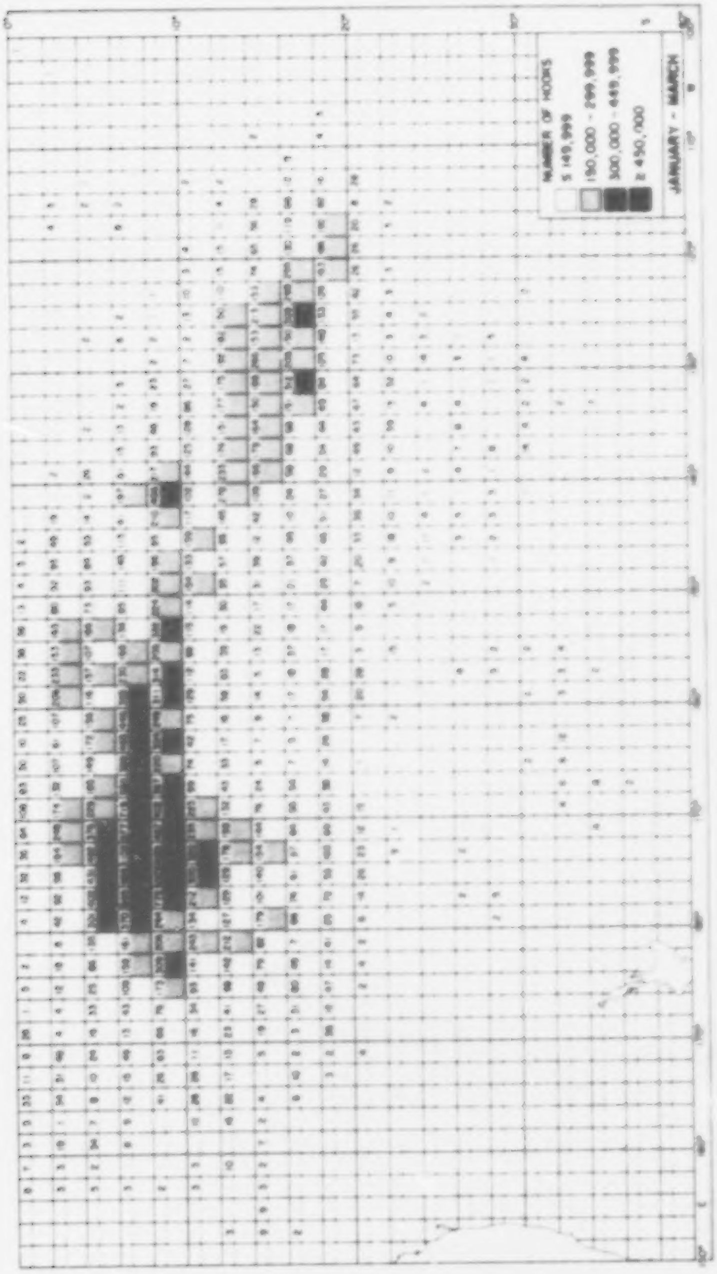
NUMBER OF HOOKS
≤ 149,999
150,000 - 299,999
300,000 - 449,999
≥ 450,000
JANUARY - MARCH

FIGURE 10.—Quarterly geographic distribution of effort, 1966-71. The numbers in the figures are in thousands.

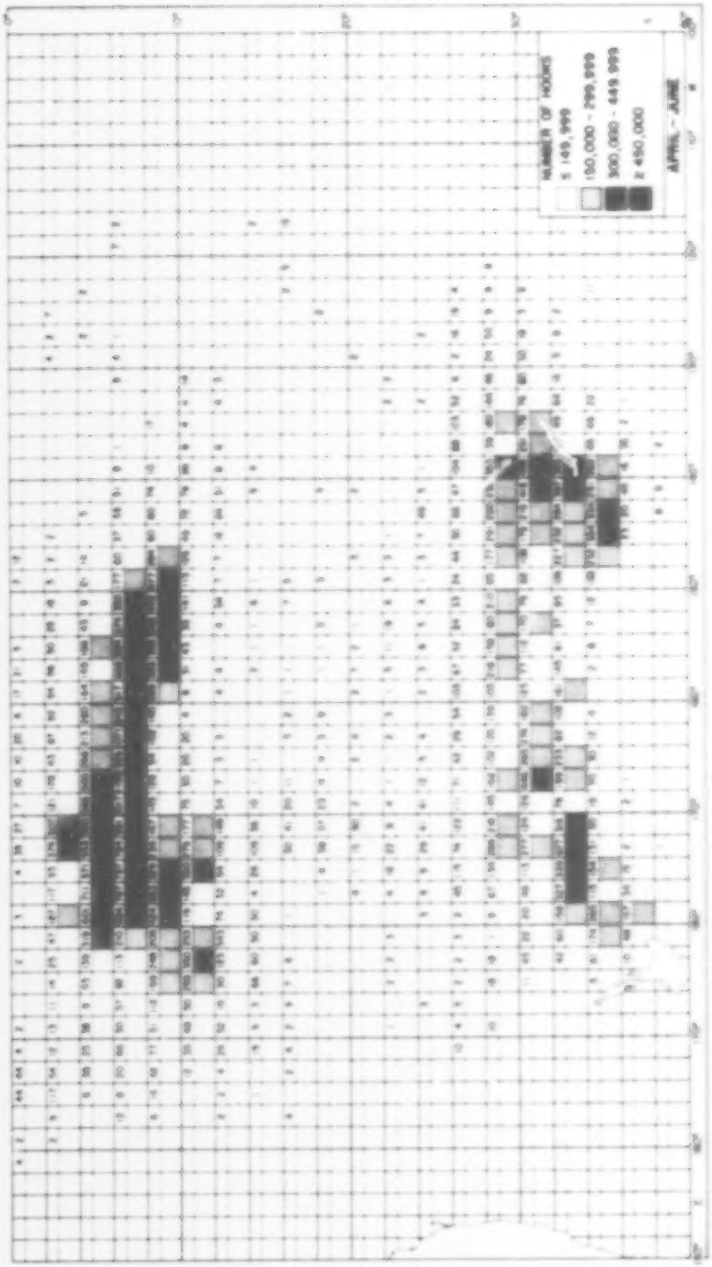
NUMBER OF HOOKS
≤ 149,999
150,000 - 299,999
300,000 - 449,999
≥ 450,000
APRIL - JUNE

FIGURE 10.—Quarterly geographic distribution of effort, 1966-71. The numbers in the figures are in thousands.—Continued

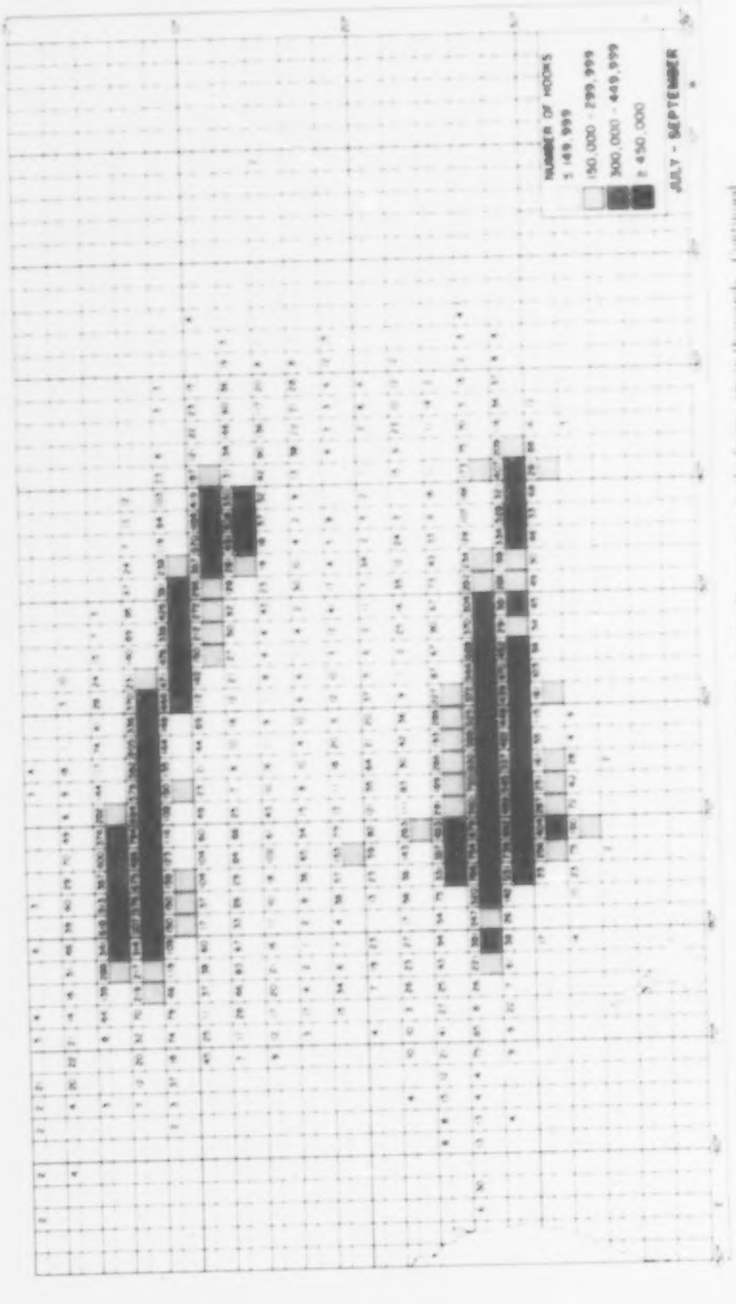
NUMBER OF HOOKS
≤149,999
150,000 - 299,999
300,000 - 449,999
≥450,000
JULY - SEPTEMBER

FIGURE 10.—Quarterly geographic distribution of effort, 1968-71. The numbers in the figures are in thousands.—Continued.

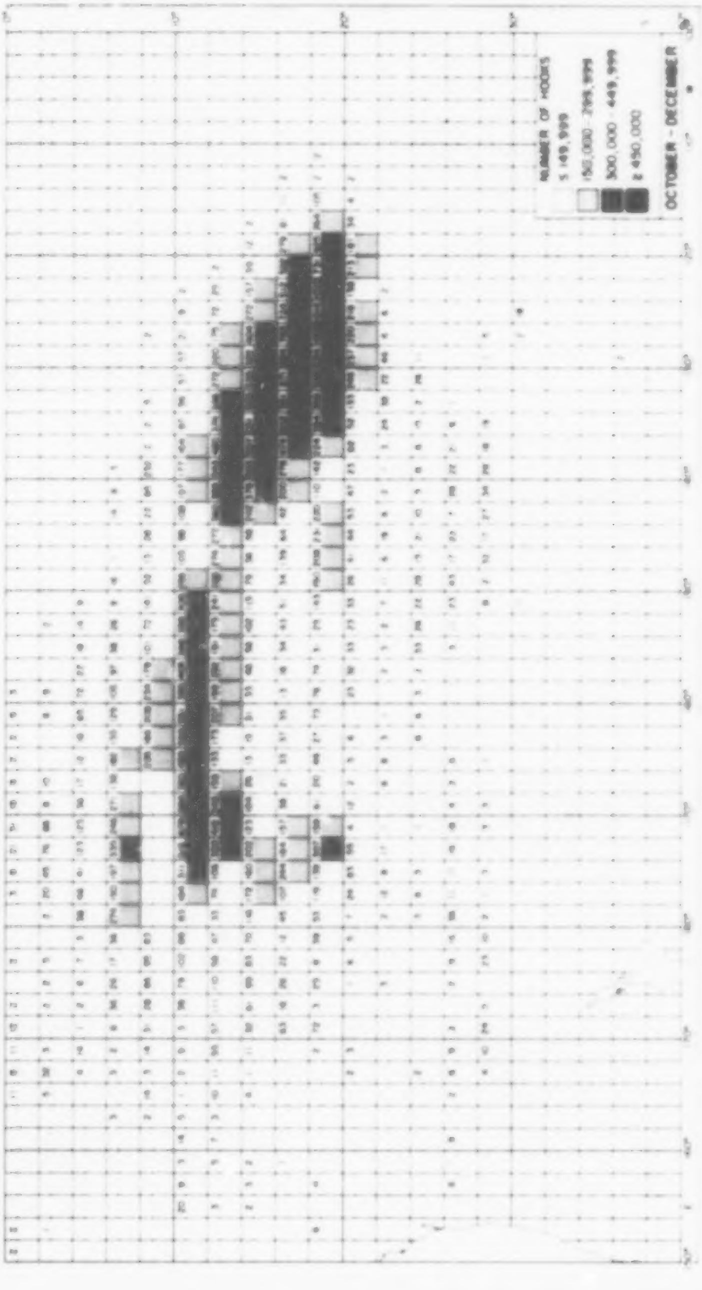
NUMBER OF HOOKS
≤ 149,999
150,000 - 299,999
300,000 - 449,999
≥ 450,000
OCTOBER - DECEMBER

FIGURE 10.—Quarterly geographic distribution of effort, 1966-71. The numbers in the figures are in thousands.—Continued.

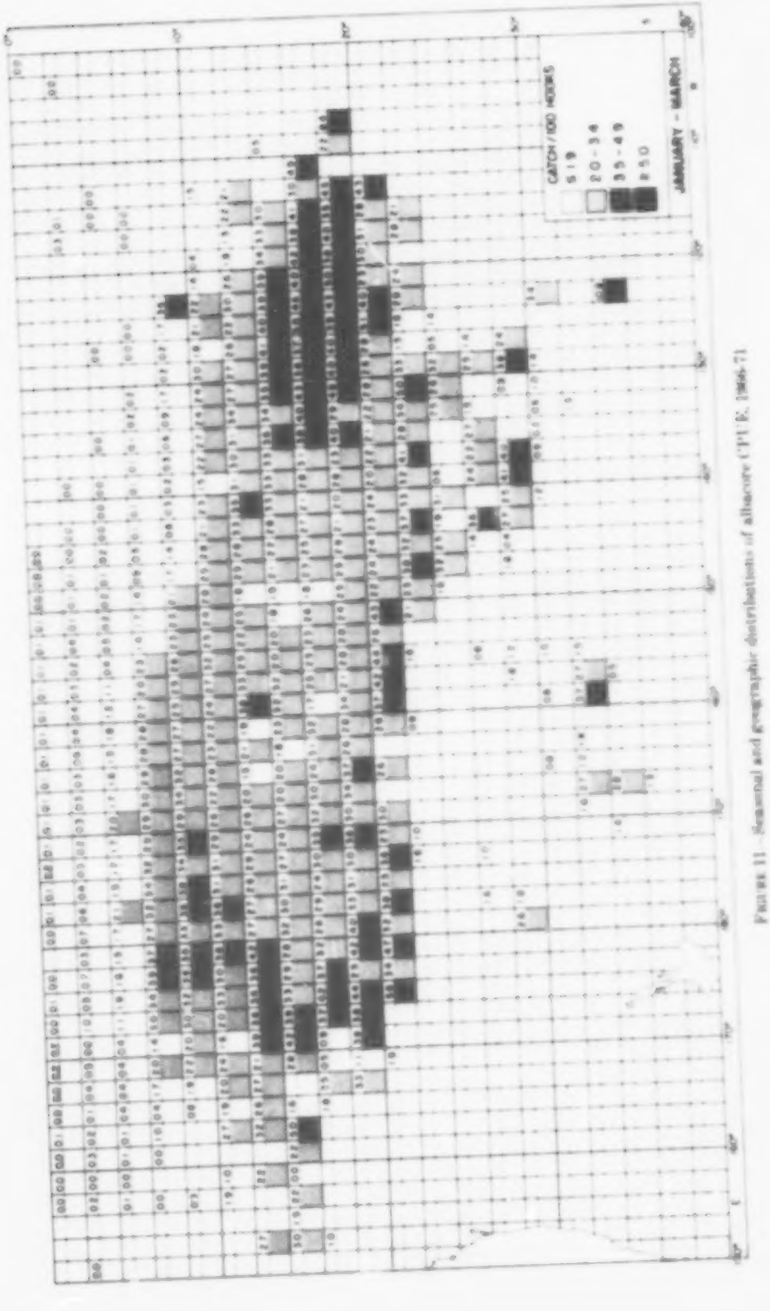
CATCH / 100 HOOKS
≤19
20-34
35-49
≥50
JANUARY - MARCH

FIGURE 11.—Seasonal and geographic distributions of albacore CPUE, 1966-71.

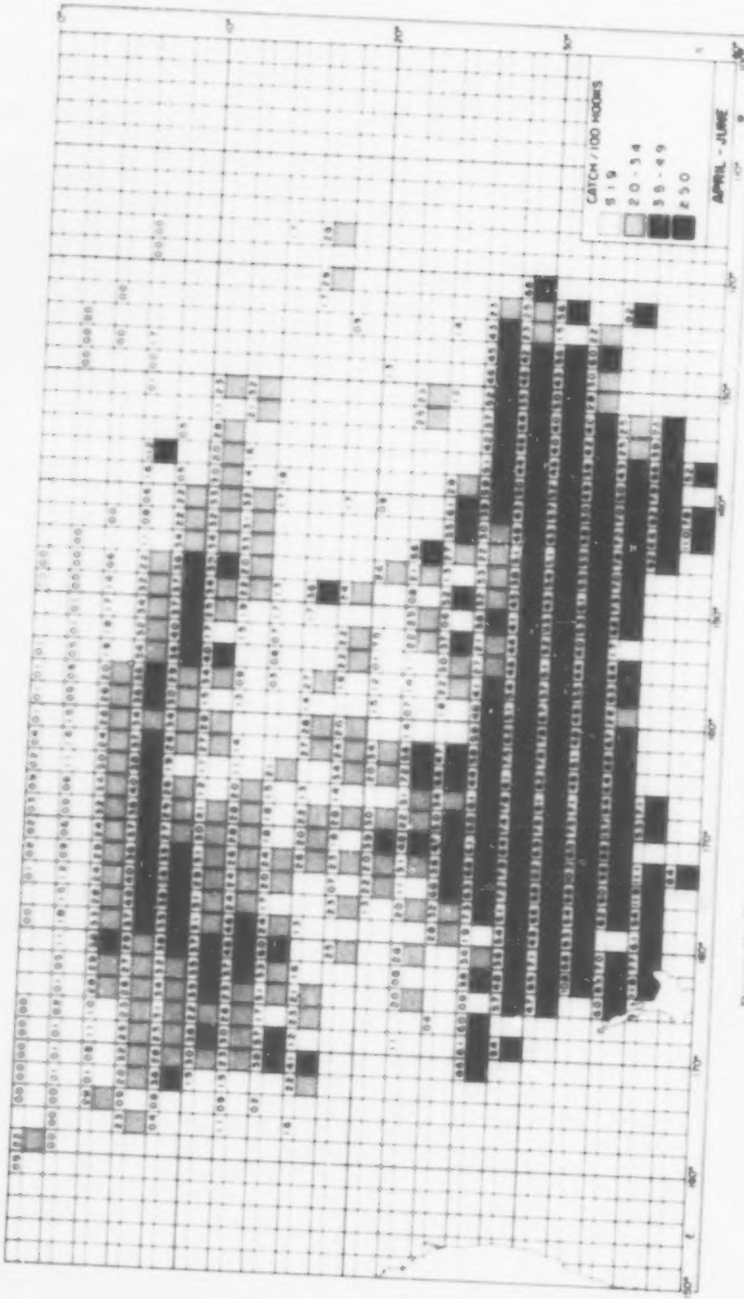
CATCH / 100 HOOKS
≤19
20-34
35-49
≥50
APRIL - JUNE

FIGURE 11.—Seasonal and geographic distributions of albacore CPUE, 1966-71—Continued.

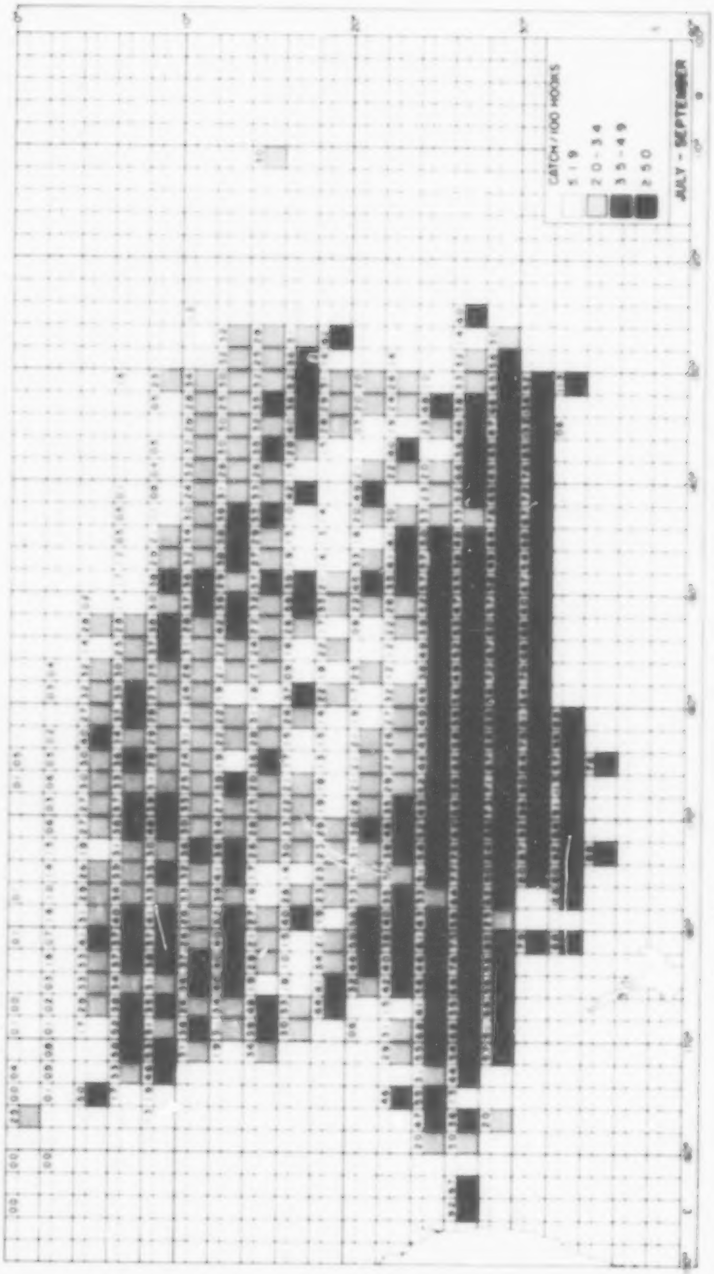
CATCH / 100 HOOKS
5-19
20-34
35-49
≥50
JULY - SEPTEMBER

FIGURE 11.—Seasonal and geographic distributions of albacore CPUE, 1968-71.—Continued.

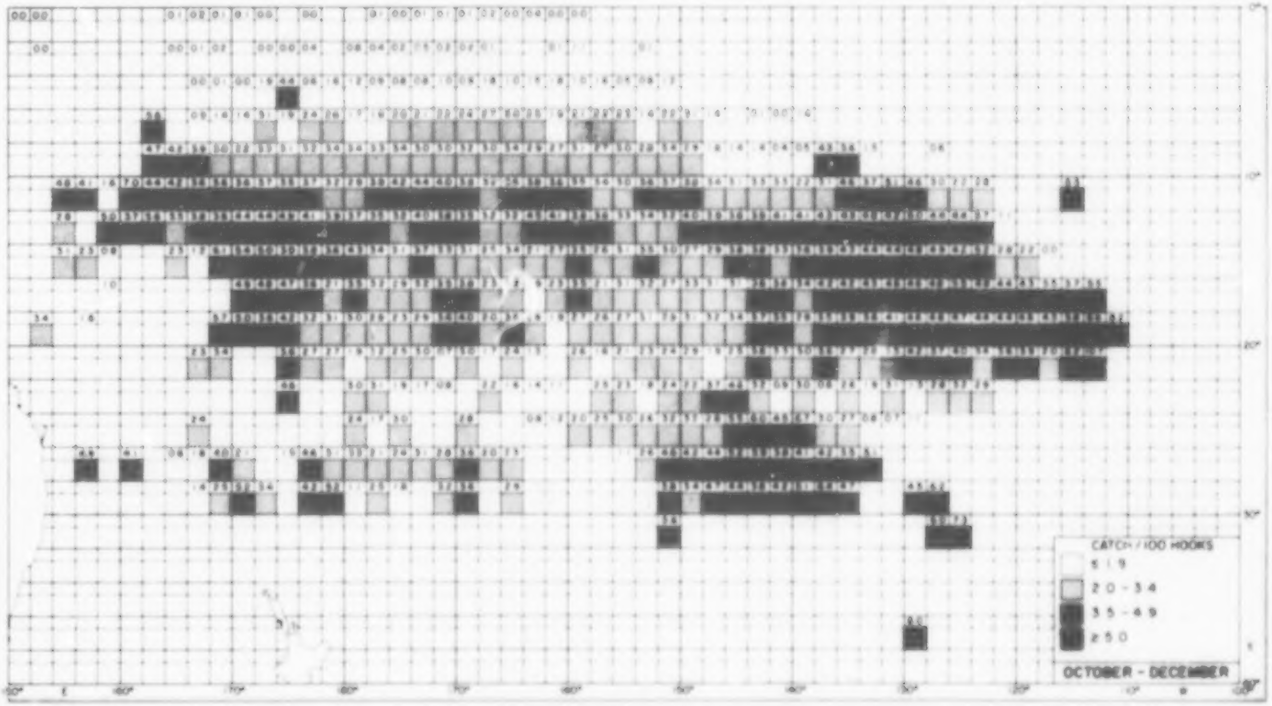
CATCH / 100 HOOKS
≤ 1 9
2 0 - 3 4
3 5 - 4 9
≥ 5 0
OCTOBER - DECEMBER

FIGURE 11.—Seasonal and geographic distributions of albacore CPUE, 1966-71.—Continued.

similar analysis covering a period from 1963 to 1965, seasonal and geographical differences in CPUE were not readily apparent (Otsu and Sumida 1968). For some reason that is not immediately clear, a distinct seasonal pattern in geographical differences in CPUE has developed in recent years. In the first quarter, there appeared to be no pattern in the distribution of areas with high CPUE (greater than five albacore per 100 hooks). However, the CPUE was better in the east-west extremes of the fishery. In the second and third quarters, an area of high CPUE developed between lat. 25° and 40°S. The fishery was also well developed north of lat. 20°S in the second and third quarters but as in the first quarter there were no well-defined areas of high CPUE. The situation in the fourth quarter reverted to approximately what it was in the first quarter. However, in some years there was a tendency for an area of high CPUE to develop in the eastern extreme of the area fished between lat. 10° and 20°S.

Because of geographical and temporal variations in the distribution of the fishing effort, the description of the geographical and temporal changes in CPUE as given above is incomplete. As noted earlier, very little fishing effort was expended south of lat. 20°S in the first and fourth quarters. It would be of interest to determine whether a high CPUE could be obtained south of lat. 20°S also in the first and fourth quarters. The possibility exists, of course, that very little effort was expended south lat. 20°S in the first and fourth quarters because the fishermen know from past experience that poor catch rates are obtained during those periods. Honma and Kamimura (1957) suggested that albacore in the South Pacific make north-south migrations and that the fishing vessels follow the movements of the albacore. In the eastern Pacific tuna fishery, Griffiths (1960) showed that the bait boat fishermen were able, on the average, to concentrate their effort on high densities of yellowfin tuna about 70% better than if their effort had been random. The data indicate that the fishermen may be able to predict the movements of the albacore with some degree of success in that areas of high fishing effort were usually associated with areas of high CPUE. There were quarters, however, in which areas of high fishing effort did not coincide with areas of high CPUE. Then, too, the fishermen may avoid fishing south of lat. 20°S in the first and fourth quarters because of bad weather or unfavorable conditions.

One other interesting observation is the division of the fishery at lat. 20°S. As noted above, the fishery develops north or south of lat. 20°S but seldom straddles it. This appears to be a well-established phenomenon, for Koto (1966) has made the same observation. Koto mentioned belts of high catch rates in the area between lat. 10° and 20°S and between lat. 20° and 30°S, and a belt of low catch rates centered at lat. 20°S. The data also indicate that the latitudinal belt centered at lat. 20°S is also a low-effort area. The causes of this phenomenon are not clear.

SIZE OF ALBACORE

Because the canneries have changed the method of handling the fish, the albacore that are sampled for length are no longer being sexed. Consequently, in the analysis of the length distribution of albacore only the data collected from 1966 to 1970, when sex data were available, are presented.

A composite length-frequency distribution of male and female albacore taken by the fishery from 1966 to 1969 is shown in Figure 12. The fish

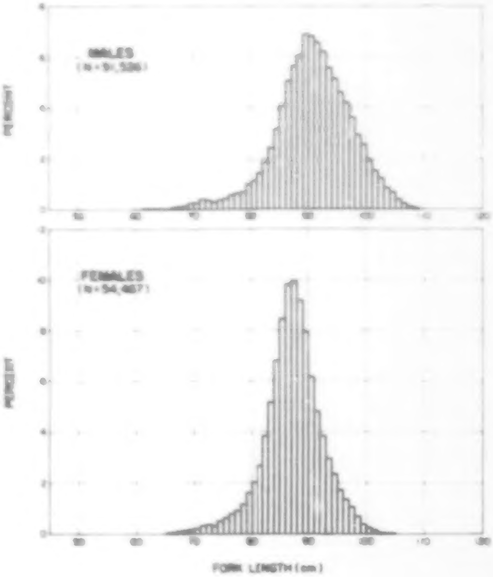

FIGURE 12.—Composite length-frequency distributions of albacore, 1966-69.

ranged in length from 50 to 129 cm. A single prominent mode was present in both the male and female distributions. For the males the mode was located at 91 cm and for the females at 88 cm.

The albacore size data were also summarized into smaller units of time and area to detect any variations which might exist. Initially the geographical area of the fishery was divided longitudinally at long. 150°W and by 10° of latitude from the equator to lat. 40°S. This was done on a quarterly basis, keeping all the years separate. This analysis did not indicate any obvious differences in the length-frequency distributions of albacore east and west of long. 150°W, nor did it show any consistent annual and seasonal differences within each geographical unit. There were, however, differences in the length-frequency distributions between the latitudinal subdivisions of the fishery. Therefore, the length data were rearranged by 10° of latitude but without regard to longitude, seasons, and year (Figure 13).

Almost without exception, the modal sizes of male albacore were larger than those of female

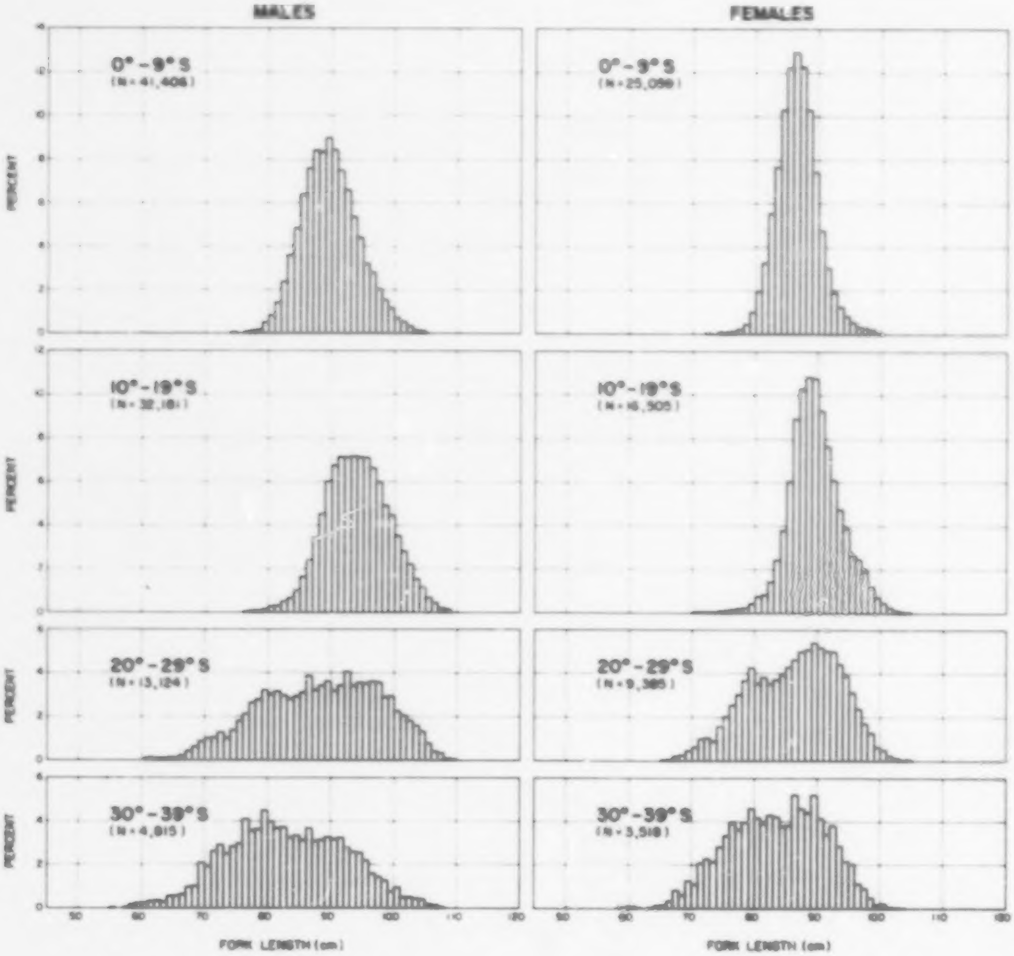

FIGURE 13.–Length-frequency distributions of albacore arranged by sex and 10° bands of latitude, 1966-70.

albacore in each of the latitudinal subdivisions. In the areas north of lat. 20°S, both male and female length-frequency distributions had a single well-defined mode. In the areas south of lat. 20°S the modes were less well defined. Koto and Hisada (1967) found a similar pattern in the length-frequency distribution of albacore in the South Pacific in 1961.

Otsu and Sumida (1968) computed the mean length of albacore in the fishery during the period from 1962 to 1965. They divided the fishery into 5° bands of latitude and noted that the fish were smallest near the equator, largest at lat. 20° to 25°S and tended to be smaller again south of lat. 25°S. The results agree in general with those of Otsu and Sumida; however, as seen above, the length-frequency distributions indicate a more complex situation than do the mean sizes. North of lat. 20°S the mean sizes may be good indicators of the general size of albacore because the length-frequency distributions showed that the fish were composed of single uniform size groups. South of lat. 20°S, the catches were composed of several size groups of fish and the mean does not indicate the presence of different size groups of fish. For example, although Otsu and Sumida stated that albacore south of lat. 25°S tended to be smaller, my data show that large fish were also present in these latitudes.

Although it is not readily apparent in the length-frequency distributions, there appears to be a declining trend in the mean size of albacore in the fishery. Otsu and Sumida (1968) noted that albacore taken in 1964 and 1965 were shorter on the average than those caught in 1963. My data show that the declining trend in the mean length of albacore has continued (Table 3).

TABLE 3.—Mean lengths of albacore, sexes combined, 1963-71.

Year	Mean length (cm)	Year	Mean length (cm)
1963	95.0	1968	89.8
1964	91.6	1969	90.4
1965	91.3	1970	88.6
1966	91.7	1971	91.5
1967	90.8		

The mechanisms that produced such a pattern in the distribution of sizes in the fishery are probably complex. The unique character of the length-frequency distributions among the four latitudinal bands must have resulted from some nonrandom distributional process. The larger numbers of smaller albacore in the more southern waters suggest that albacore are initially recruited into the fishery in the area south of lat. 20°S. The high CPUE experienced in the second and third quarters south of lat. 20°S may be an indication of this. Also, it has been shown that juvenile albacore which originate from spawning that takes place north of lat. 20°S migrate south as they grow larger (Yoshida 1971).

SUMMARY

A comparison of various indices of apparent abundance of albacore indicated that catch per day and catch per 100 hooks were better indicators of apparent abundance than catch per trip. The mean catch per day and catch per 100 hooks of albacore have generally declined over the years, which suggests that the apparent abundance of albacore has declined in the American Samoa longline fishery. To compensate for the reduced CPUE, the longliners fished more days per trip and traveled farther from the home base seeking areas of good catch rates.

The fishery apparently has had an effect on the albacore stock. Although the annual landings have continued to increase with increased fishing effort, the CPUE has declined. That the apparent overall effect was not greater was due to the fact that the fishing grounds have expanded, especially into areas south of lat. 20°S where good catch rates were obtained. The mean annual CPUE plotted against fishing effort for selected, discrete areas north and south of lat. 20°S indicated that the fishery has not as yet had as great an effect in the south as it has to the north. There are at least two possible reasons for the better condition of the fishery to the south. First, the area south of lat. 20°S has not been exploited as long as the area to the north. Second, it was shown that the albacore are first recruited into the fishery in the latitudes south of lat. 20°S, which may account in part for the higher apparent abundance.

There was some indication that there were temporal changes in apparent abundance of albacore south of lat. 20°S. Because of poor weather conditions or because the fishermen have learned through experience that catch rates are better during certain seasons, or a combination of these and other reasons, fishing effort expended south of lat. 20°S fluctuates seasonally. Areas of concentrated fishing effort were evident in the second and third quarters in the area south of lat. 20°S. Very little effort was expended in these waters in the first and fourth quarters. Good CPUE's were experienced in these areas of high fishing effort in the second and third quarters. Although there were some indications that the apparent abundance of albacore was low in the southern waters in the first and fourth quarters, more data are needed to show this conclusively.

The apparent temporal changes in CPUE in the southern waters may be related to seasonal changes in recruitment of albacore into the fishery. The length-frequency distribution of albacore in waters south of lat. 20°S showed that several size groups of fish were represented in the catches, including groups of small fish not found north of lat. 20°S. The good CPUE in the second and third quarters may indicate periods of active recruitment. Generally, the albacore were stratified by size latitudinally; however, no such stratification was evident longitudinally. North of lat. 20°S the catches were composed of fish of a single size group. South of this latitude, as already indicated, the catches were composed of several size groups of fish.

ACKNOWLEDGMENTS

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LITERATURE CITED

Griffiths, R. C.
1960. A study of measures of population density and of concentration of fishing effort in the fishery for yellowfin tuna, *Neothunnus macropterus*, in the Eastern Tropical Pacific Ocean, from 1951 to 1956. Inter-Am. Trop. Tuna Comm. Bull. 4:41-136.

Honma, M., and T. Kamimura.
1957. Studies on the albacore. V. The fishing condition and size of albacore taken in the South Pacific Ocean. [In Jap., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 6:84-90.

Koto, T.
1966. Studies on the albacore. XI. Distribution of albacore in the tuna longline fishing grounds of the South Pacific Ocean. [In Jap., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 23:43-53.

Koto, T., and K. Hisada.
1967. Studies on the albacore. XIII. Size composition of South Pacific albacore caught by longline. [In Jap., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 25:37-47.

Otsu, T., and R. F. Sumida.
1968. Distribution, apparent abundance, and size composition of albacore (*Thunnus alalunga*) taken in the longline fishery based in American Samoa, 1954-65. U.S. Fish Wildl. Serv., Fish. Bull. 67:47-69.

Rothschild, B. J.
1967. Competition for gear in a multiple-species fishery. J. Cons. 31:102-110.

Skillman, R. A.
1975. An assessment of the South Pacific albacore, *Thunnus alalunga*, fishery, 1953-72. Mar. Fish. Rev. 37(3):9-17.

Suda, A.
1971. Tuna fisheries and their resources in the IPFC area. [Jap. summ.] Far Seas Fish. Res. Lab. (Shimizu), S Ser., 5, 58 p.

Suzuki, G.
1961. On tuna fishing at the Samoa base in 1956. [In Jap.] Tuna Fish. (Maguro Gyogyō) 76:13-18.

Yoshida, H. O.
1971. Distribution, apparent abundance, and length composition of juvenile albacore, *Thunnus alalunga*, in the South Pacific Ocean. Fish. Bull., U.S. 69:821-827.

EFFECTS OF PHOTOPERIOD-TEMPERATURE REGIMES AND PINEALECTOMY ON BODY FAT RESERVES IN THE GOLDEN SHINER, *NOTEMIGONUS CRYSOLEUCAS*

VICTOR L. DE VLAMING[1]

ABSTRACT

Various photoperiod-temperature regimes were examined for their effects on total fat content (excluding gonads) in *Notemigonus crysoleucas*; experiments were conducted during several different phases of the reproductive cycle. In *Notemigonus*, fattening normally occurs in fall and early winter concomitant with the early phases of gonadal development. Body fat stores are progressively depleted during the prespawning and spawning seasons. Warm temperature (25°C) normally favored body fat depletion in *Notemigonus*. Short photoperiod (9L/15L) accentuated the lipid depleting effects of warm temperatures. Low temperatures (12°-15°C) usually promoted lipid deposition. Short photoperiods complimented the lipid anabolic effects of low temperatures. Thus, a given photoperiod can have opposite effects on body fat levels depending on temperature. A long photoperiod, in combination with warm temperatures, is required for final gonadal maturation and results in a reduction of lipid reserves. Short photoperiod-warm temperature regimes have similar effects on fat levels, but bring about gonadal regression. Thus, the effects of photoperiod-temperature regimes on lipid metabolism are apparently not totally dependent on the effects of these environmental factors on reproduction.

The effects of pinealectomy on lipid reserves varied depending on the phase of the natural reproductive cycle when the organ was removed, as well as, with the photoperiod-temperature regime under which the experimental animals were maintained. At 25°C and under a 15.5L/8.5D photoperiod, fat levels were frequently lower in pinealectomized than in sham animals. The opposite was usually true for fish exposed to a 9L/15D-25°C regime. Lipid reserves were normally greater in pinealectomized than in sham operated fish maintained on 15.5L/8.5D-12°C regime. Body fat composition was frequently less in pinealectomized than in sham operated animals exposed to a 9L/15D-12°C regime. Pinealectomy reverses the effects of photoperiod on lipid metabolism at a particular temperature. These results suggest that the pineal body is involved in regulating physiological functions and may serve as a photoreceptor and/or transducer of photoperiod information.

In most temperate-latitude aquatic environments food availability varies seasonally and annual cycles of growth, reproduction, and fattening are normally observed in teleost fishes. Lipid reserves may be used to meet the energy demands of reproduction, and seasonal fattening cycles in teleosts may be related to sexual cycling (Lovern 1934; Lühmann 1953; Love 1957; Idler and Bitners 1960; Woodhead 1960; Nikolsky 1963; Wilkins 1967; Lasker 1970; de Vlaming 1971). Environmental factors such as photoperiod and temperature are used as cues to maintain annual reproductive cycles in fishes (for reviews see de Vlaming 1972, 1974), but little is known about environmental control of fattening.

The pineal body of most fishes has sensory organ characteristics (e.g., Rüdeberg 1966, 1969; Omura and Oguri 1969; Owman and Rüdeberg 1970; Bergmann 1971; Oksche et al. 1971). Histological examination of the pineal in various teleosts also reveals secretory gland characteristics (e.g., Takahashi 1969; Chèze and Lahaye 1969; Chèze 1970; Rizkalla 1970; Hafeez 1971). In mammals the pineal appears to function as an endocrine gland and the indolamine, melatonin, may be one of the hormones of this organ (cf. Reiter 1973). Histochemical and biochemical data show that the teleost pineal has an active indolamine metabolism (Quay 1965; Hafeez and Quay 1969, 1970; Fenwick 1970; Owman and Rüdeberg 1970). Very little, however, is known about the physiological role of the pineal in teleost fishes.

De Vlaming, Sage, Charlton, and Tiegs (1974) showed that melatonin treatment results in body lipid depletion in *Fundulus similis* and *Cyprinodon variegatus* acclimated to a long photoperiod. In *F. similis* acclimated to a short photoperiod during May, melatonin therapy also resulted in fat depletion, but body fat deposition

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was observed in *F. similis* acclimated to a short photoperiod during July and treated with this indolamine (de Vlaming, Sage, Charlton, and Tiegs 1974). These investigators concluded that the pineal might be somehow involved in regulating body fat reserves in teleosts. The data of de Vlaming, Sage, Charlton, and Tiegs (1974) and others (Fenwick 1970; Urasaki 1972a, b, c) indicate that the influence of the pineal on physiological functions in teleosts may vary depending on season and photoperiod conditions.

The objectives of the present investigation were to examine the effects of various photoperiod-temperature regimes on body lipid reserves in the cyprinid teleost *Notemigonus crysoleucas* and to determine if pinealectomy altered the response of this fish to the experimental regimes. The possible relationship between reproductive activity and body fat reserves was also examined. That is, the effects of photoperiod-temperature regimes and pinealectomy on reproductive activity were determined and compared to the data on fat metabolism. The effects of pinealectomy on reproductive activity and fattening were examined during different phases of the natural sexual cycle (at various times of the year) to determine if physiological responses vary seasonally.

MATERIALS AND METHODS

Samples of *N. crysoleucas* were collected in ponds around the area of Menomonee Falls, Wis. (lat. 43°10'N) at several different times during the year. The reproductive cycle consists of a spawning season which extends from May through July. There is a postspawning season during August and September in which the gonads regress. From October through February there is a gonadal preparatory period, in which spermatogonia proliferate slowly and spermatocytes appear in the testes. Vitellogenesis is initiated during this period. March and April can be referred to as the prespawning period; during this time, final gonadal maturation occurs (i.e., spermatozoa fill the testes and ovaries are distended with mature oocytes). Several fish from each field sample were sacrificed, the gonads examined and body lipid levels determined at the time of collection; these fish served as a reference for the experiments that followed. In the following discussion the fish sacrificed at the time of collection will be identified as initial controls.

Sham operated and pinealectomized fish were maintained under various photoperiod and constant temperature regimes (see Results) in 114- or 285-liter tanks supplied with aerated and filtered dechlorinated tap water. Temperatures selected for these experiments are within the range normally experienced during the year in nature by this species. Illumination was a combination of incandescent and cool white fluorescent bulbs which gave a light intensity of 200 to 275 lx at the surface of each tank. Fish were fed ad libitum on a commercial fish food (Tetra-Min)[2]; animals maintained at warm temperatures were fed twice daily whereas fish at low temperatures were fed only once a day. All *Notemigonus* used in these studies weighed between 12 and 17 g.

For pinealectomies, fish were anesthetized in buffered tricaine methane-sulfonate (1:4,000). Each fish was then wrapped in cheesecloth and submerged in water so that only the top of the skull was emergent. The section of skin covering the pineal area was cut and folded back to reveal the parietal bone. Using a diamond-edged wheel saw (diameter = 2.2 cm) attached to a dental drill, three sides of a rectangle (5×4 mm) were cut in the parietal bone. This bone flap was then lifted forward toward the animal's mouth to expose parts of the cerebrum and midbrain. The pineal could then be easily removed using a gentle suction applied through a Pasteur pipette. After removal of the pineal, the parietal bone and the epithelial flaps were individually sealed into place with Eastman's 910 Adhesive. Sham operations consisted of raising the parietal bone flap without removing the pineal. Removal of the pineal can be completed within 2 min in this species.

The effects of pinealectomy on reproductive function were assessed by gravimetric and histological techniques. Fish were sacrificed by severing the spinal cord. Body weight and gonadal weight were recorded immediately after sacrifice. Gravimetric data are expressed in terms of the gonosomatic index (GSI) (gonadal weight/body weight × 100) since gonadal size in this species depends on body weight. After weighing, gonads were fixed in Bouin's solution and embedded in paraplast for histological examination. The data obtained on the effects of pinealectomy on reproductive function in *Notemigonus* are the subject of another report (de Vlaming 1975). GSI data are presented here without statistical comparisons or extensive discussion so that comparisons can be made with the results on body lipid reserves. After removal of the gonads, the bodies of the fish were extracted to remove lipids. The procedure used to measure body fat content has been previously described (de Vlaming, Sage, Charlton, and Tiegs 1974; de Vlaming et al. in press). Basically this technique consists of extracting in a methanol:chloroform:ether solution (1:1:1). Body fat content is expressed as a function of dry body weight.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Preparatory Season

The effects of pinealectomy on body lipid reserves were first examined during the gonadal preparatory period (January). The results of this experiment are summarized in Table 1.

Body lipid reserves were significantly depleted in both male and female sham operated fish maintained at 25°C (whether on a long or short photoperiod) compared to the initial January controls.

TABLE 1.–The effects of pinealectomy on body lipid reserves in *Notemigonus* maintained on various photoperiod-temperature regimes during the gonadal preparatory season (30-day treatment).

Treatment	n	Sex	Dry lipid index[1] $\overline{X} \pm$ SE	Gonosomatic index[2] $\overline{X} \pm$ SE
Initial controls	5	M	248 ± 11	1.48 ± 0.09
(January)	9	F	207 ± 10	3.03 ± 0.25
15.5L/8.5D photoperiod:				
25°C:				
Sham operated	6	M	136 ± 7	2.82 ± 0.07
	9	F	164 ± 11	4.67 ± 0.42
Pinealectomized	5	M	119 ± 5*	0.34 ± 0.18
	10	F	139 ± 8*	2.88 ± 0.37
12°C:				
Sham operated	6	M	235 ± 10	1.95 ± 0.16
	8	F	211 ± 7	3.42 ± 0.08
Pinealectomized	6	M	246 ± 9	1.20 ± 0.04
	10	F	237 ± 5*	3.47 ± 0.13
9L/15D photoperiod:				
25°C:				
Sham operated	5	M	116 ± 8	0.94 ± 0.09
	8	F	96 ± 6	1.78 ± 0.22
Pinealectomized	6	M	106 ± 5	0.89 ± 0.16
	9	F	109 ± 11	1.64 ± 0.21
12°C:				
Sham operated	6	M	263 ± 12	1.28 ± 0.11
	10	F	244 ± 9	3.40 ± 0.21
Pinealectomized	5	M	250 ± 15	1.19 ± 0.18
	8	F	221 ± 6*	4.12 ± 0.35

[1] Dry lipid index = mg lipid, less gonadal lipids/g dry body wt.
[2] Gonosomatic index = wt of gonads (g)/g body wt x 100.
*Significantly ($P < 0.05$) different than sham operated controls maintained under same photoperiod-temperature regime.

In both sexes of sham operated fish exposed to the long photoperiod-low temperature regime body lipid stores were maintained at the initial levels. Short photoperiod-low temperature treatment, however, caused a significant increase in fat stores in sham operated females, but not in sham operated males.

In sham operated control fish maintained on a long photoperiod, body lipid levels were significantly higher in the group at 12°C than in the group at 25°C. Fat levels were also significantly greater in sham operated *Notemigonus* maintained at 12°C than at 25°C on a short photoperiod. These data suggest that low temperatures, regardless of daylength, either maintain or favor body lipid deposition in this species.

At 12°C, a short photoperiod was more effective in maintaining or stimulating lipid deposition than a long photoperiod. Specificially, body fatness (in both sexes) was significantly greater in sham operated fish exposed to the short photoperiod-low temperature regime than in animals maintained on the long photoperiod-low temperature regime. Thus, short daylengths seem to compliment the effects of low temperatures on fat deposition. Body lipid levels were significantly lower in sham operated animals maintained on the short photoperiod-warm temperature regime than in fish exposed to the long photoperiod-warm temperature regime. Body fat depletion in *Notemigonus* at warm temperatures is therefore accentuated by short daylengths.

In animals maintained on the 15.5L/8.5D-25°C regime, body lipid levels were significantly lower in the pinealectomized group than in sham operated group. Pinealectomy also retarded fat deposition in female fish exposed to the 9L/15D-12°C regime. In contrast, body fat levels were significantly greater in the female pinealectomized fish than in the sham operated females maintained on the long photoperiod-low temperature regime. Body lipid levels in pinealectomized fish did not differ significantly from lipid levels in control sham operated animals under any of the other experimental conditions. These data suggest that the effects of pinealectomy on lipid metabolism depend on photoperiod and temperature conditions.

The effects of pinealectomy on reproductive function are discussed elsewhere (de Vlaming 1975). One should note, however, that pinealectomy retarded the stimulatory effects of the 15.5L/8.5D-25°C regime on gonadal maturation under these same conditions body lipid levels were also significantly lower in pinealectomized than in sham operated fish. Ovarian GSI was significantly higher in the pinealectomized than in sham operated group exposed to the 9L/15D-12°C regime; however, body fat levels were significantly lower in pinealectomized than in sham operated fish under these conditions. These data imply that the effects of pinealectomy on lipid deposition do not necessarily depend on the effects of this organ on reproductive activity.

Prespawning Season

The effects of pinealectomy on body fat reserves were examined again during the prespawning season (Table 2).

Regardless of photoperiod, low temperature treatment of both sexes of sham operated *Notemigonus* resulted in a significant increase in body fatness, compared to the initial March controls. Warm temperature treatment, however, caused a depletion of body lipids in sham operated fish compared to the initial controls; this fat depletion was observed in both photoperiod groups.

Body fatness (in females) was significantly greater in sham operated control fish exposed to the 9L/15D-12°C regime than in animals maintained on the 15.5L/8.5D-12°C regime. These data further confirm the suggestion that short daylengths compliment the effects of low temperatures on fattening. Body lipid levels (both sexes) were significantly lower in sham operated animals maintained on the short photoperiod-warm temperature regime than in sham operated fish exposed to the long photoperiod-warm temperature regime. The lipid depletion which occurs at warm temperatures is thus accentuated by short daylengths.

Body fat levels (both sexes) were significantly lower in the pinealectomized group than in the sham operated group maintained on the 15.5L/8.5D-25°C regime. In animals maintained on a long photoperiod-low temperature regime, body lipid levels were significantly greater in the pinealectomized fish than in the shams. Pinealectomized females contained significantly more fat than sham operated females exposed to the short photoperiod-warm temperature regime. In contrast, body lipid levels (both sexes) were significantly lower in pinealectomized than in sham operated fish maintained on the 9L/15D-12°C regime. At a low temperature, pinealectomy interferes with the complimentary effects of short photoperiods on lipid deposition. At a warm temperature, however, pinealectomy reverses the accentuating effects of short photoperiods on body lipid depletion.

TABLE 2.–The effects of pinealectomy on body lipid reserves in *Notemigonus* maintained on various photoperiod-temperature regimes during the prespawning season (21-day treatment).

Treatment	n	Sex	Dry lipid index[1] $\bar{X} \pm SE$	Gonosomatic index[2] $\bar{X} \pm SE$
Initial controls	5	M	209 ± 10	1.96 ± 0.17
(March)	9	F	184 ± 12	3.42 ± 0.09
15.5L/8.5D photoperiod:				
25°C:				
Sham operated	6	M	140 ± 11	1.35 ± 0.07
	8	F	131 ± 5	2.41 ± 0.15
Pinealectomized	6	M	112 ± 10*	0.80 ± 0.09
	7	F	107 ± 8*	1.58 ± 0.22
12°C:				
Sham operated	6	M	232 ± 8	2.00 ± 0.10
	7	F	244 ± 7	3.41 ± 0.26
Pinealectomized	6	M	251 ± 6*	1.79 ± 0.14
	7	F	264 ± 7*	3.18 ± 0.33
9L/15D photoperiod:				
25°C:				
Sham operated	8	M	129 ± 5	2.02 ± 0.15
	6	F	114 ± 6	1.74 ± 0.11
Pinealectomized	6	M	143 ± 9	1.62 ± 0.04
	7	F	132 ± 8*	2.03 ± 0.13
12°C:				
Sham operated	5	M	243 ± 5	1.31 ± 0.05
	5	F	267 ± 8	3.79 ± 0.28
Pinealectomized	6	M	187 ± 11*	1.20 ± 0.07
	4	F	240 ± 6*	3.43 ± 0.27

[1] Dry lipid index = mg lipid, less gonadal lipids/g dry body wt.
[2] Gonosomatic index = wt of gonads (g)/g body wt x 100.
*Significantly ($P < 0.05$) different than sham operated controls maintained under same photoperiod-temperature regime.

Interestingly, body lipid levels in pinealectomized females maintained on the 9L/15D-12°C regime did not differ significantly from fat levels in sham operated females exposed to the 15.5L/8.5D-12°C regime. Fat levels were not significantly different in pinealectomized females on the 15.5L/8.5D-12°C regime and sham operated females on the 9L/15D-12°C regime. Similarly, body fat levels in pinealectomized fish (both sexes) exposed to the 9L/15D-25°C regime did not differ significantly from lipid levels in shams maintained on the 15.5L/8.5D-25°C regime. These data indicate that pinealectomy reverses the effects that photoperiod has on lipid levels at a given temperature.

Pinealectomy reverses the stimulatory effects of a long photoperiod-warm temperature regime, causing gonadal regression (de Vlaming 1975); under these conditions body lipid levels in pinealectomized animals are lower than in shams. Short photoperiods in combination with warm temperatures induce gonadal involution in *Notemigonus*. Pinealectomy under these conditions prevents gonadal regression, stimulating gonadal development and spawning. Body lipid reserves were significantly greater in pinealectomized fish than in shams maintained on the 9L/15D-25°C regime. Under the other photoperiod-temperature regimes, pinealectomy resulted in changes in body fat reserves without appreciably altering reproductive activity. Possibly then, changes in lipid metabolism due to pinealectomy may influence reproductive activity, but apparently the effects of pinealectomy on fat deposition are not totally dependent on changes in sexual activity.

Spawning Season

The effects of pinealectomy on body fat stores were again examined during the early spawning season (late April, Table 3).

In sham operated fish maintained at 25°C (both photoperiod groups), the lipid index was significantly lower than that of the initial controls. Body lipid reserves were also significantly depleted in sham operated female fish exposed to the 9L/15D-25°C regime, but not in sham operated females maintained on the 15.5L/8.5D-25°C regime compared to the initial controls. Low temperature treatment during the spawning season caused a significant increase in body lipid content of sham operated female fish regardless of photoperiod. The short photoperiod-low temperature regime stimulated fat deposition in sham operated males; however, body lipid levels did not differ significantly in the initial controls and sham operated males maintained on the long photoperiod-low temperature regime.

TABLE 3.–The effects of pinealectomy on body lipid reserves in *Notemigonus* maintained on various photoperiod-temperature regimes during the early spawning season (21-day treatment).

Treatment	*n*	Sex	Dry lipid index[1] $\bar{X} \pm$ SE	Gonosomatic index[2] $\bar{X} \pm$ SE
Initial controls	6	M	91 ± 2	3.10 ± 0.22
(Late April)	8	F	98 ± 3	6.53 ± 0.97
15.5L/8.5D photoperiod:				
25°C:				
Sham operated	7	M	56 ± 4	2.79 ± 0.25
	7	F	87 ± 6	5.13 ± 1.04
Pinealectomized	5	M	45 ± 5	2.10 ± 0.09
	8	F	62 ± 4*	4.08 ± 0.73
15°C:				
Sham operated	5	M	91 ± 5	2.16 ± 0.09
	6	F	114 ± 6	5.88 ± 0.89
Pinealectomized	5	M	132 ± 8*	2.38 ± 0.14
	6	F	129 ± 6*	7.81 ± 1.22
9L/15D photoperiod:				
25°C:				
Sham operated	5	M	68 ± 5	1.16 ± 0.15
	9	F	74 ± 6	2.87 ± 0.52
Pinealectomized	6	M	110 ± 6*	2.67 ± 0.16
	5	F	101 ± 7*	3.50 ± 0.88
15°C:				
Sham operated	6	M	155 ± 10	3.12 ± 0.17
	5	F	138 ± 8	6.43 ± 0.66
Pinealectomized	5	M	124 ± 9*	3.01 ± 0.15
	7	F	117 ± 5*	5.89 ± 0.57

[1] Dry lipid index = mg lipid, less gonadal lipids/g dry body wt.

[2] Gonosomatic index = wt of gonads (g)/g body wt x 100.

*Significantly ($P < 0.05$) different than sham operated controls maintained under same photoperiod-temperature regime.

At 25°C, body lipid stores were slightly higher in sham operated female fish maintained on a long photoperiod than in females exposed to a short photoperiod; the reverse was true for males. At 15°C, sham operated fish maintained on a short photoperiod were significantly fatter than sham operated fish on the long photoperiod regime.

Lipid reserves were significantly lower in female pinealectomized than in sham operated female fish exposed to the 15.5L/8.5D-25°C regime. In fish (both sexes) maintained on the long photoperiod-low temperature regime, body lipid stores were significantly greater in pinealectomized than in sham operated control fish. Body fat content was significantly greater in both sexes of pinealectomized fish than in shams exposed to the 9L/15D-25°C regime. In contrast, lipid content in pinealectomized fish was significantly lower than in sham operated animals on the 9L/15D-15°C regime.

Body lipid reserves were not significantly different in pinealectomized female fish maintained on the 9L/15D-15°C regime compared to the females exposed to the 15.5L/8.5D-15°C regime. Fat composition of pinealectomized females exposed to the long photoperiod-low temperature regime did not differ significantly from fat composition in sham operated females which experienced the short photoperiod-low temperature regime. No significant difference was observed in body fatness in pinealectomized females on the 9L/15D-25°C regime and sham operated females on the 15.5L/8.5D-25°C regime. Similarly, body lipid stores were approximately the same in pinealectomized females maintained on the long photoperiod-warm temperature regime and in sham operated females exposed to the short photoperiod-warm temperature regime.

Many of the fish maintained on the 15.5L/8.D-25°C regime spawned; under these conditions pinealectomy resulted in the initiation of gonadal regression. Compared to sham operated animals exposed to the long photoperiod, body lipid levels in pinealectomized fish were significantly lower. Gonadal regression was also initiated in sham operated fish maintained on the 9L/15D-25°C regime; spawning was observed in pinealectomized animals on this regime. Body lipid levels were significantly greater in pinealectomized fish than in sham operated fish maintained on the short photoperiod-warm temperature regime. In animals maintained at a low temperature (both photoperiods), GSIs did not differ significantly in the pinealectomized and sham operated groups. Sham operated fish, however, were significantly fatter than the pinealectomized animals experiencing the 9L/15D-15°C regime. Furthermore, under the 15.5L/8.5D-15°C regime, pinealectomized fish contained significantly more fat than the sham operated controls.

DISCUSSION

Both temperature and photoperiod have a distinct effect on body lipid reserves in *N. crysoleucas*. During the prespawning and spawning seasons, low temperature treatment (12°-15°C) favors increases in body fat stores in both sexes of *Notemigonus*, regardless of photoperiod conditions. Low temperature treatment of *Notemigonus* during the gonadal preparatory season did not result in lipid deposition, but did maintain body fat composition at a level equivalent to that in the initial controls (sacrificed at the onset of the experiment). Animals collected during the preparatory period (January) were very fat. In fact, body fat stores in this species reach a peak in late December, January, and early February. The failure of laboratory low temperature treatment to stimulate lipid deposition during the preparatory season could be due to the presence of sufficient fat reserves in the initial controls. Regardless of season or photoperiod, high temperature (25°C) acclimation favors body lipid depletion in males. During the preparatory and prespawning seasons, body fat depletion is also observed in females exposed to warm temperatures. Compared to initial controls (animals sacrificed at the beginning of the experiment), lipid levels in *Notemigonus* maintained at warm temperatures during the early spawning season were not appreciably altered. The failure of warm temperature treatment to deplete lipid reserves in females during the early spawning season may be due to the relatively low levels of fat in the initial controls. Fish maintained at warm temperatures were fed twice daily whereas fish exposed to low temperatures were fed only once a day; warm temperature animals consumed four to five times more food than the low temperature fish. Since the fish in all experiments were fed ad libitum, the differences in body lipid levels should not be due entirely to higher metabolic rates at elevated temperatures. Lipid synthesis and deposition is also promoted at low temperatures in several other teleost species (Blazka 1958; Brown 1960; Dean and Goodnight 1964; Knipprath and Mead 1968; de Vlaming and Pardo 1975). The means by which temperature acts to control lipid metabolism is not fully understood, but Kinne (1960) reported that the efficiency of food conversion in *Cyprinodon macularis* is maximal at lower temperatures. Furthermore, enzyme systems (Hochachka 1969) and hormones (de Vlaming and Pardo 1975; Pardo and de Vlaming in press) involved in lipid metabolism in fishes appear to be temperature sensitive.

At low temperatures, short photoperiods are more effective than long photoperiods at stimulating lipid deposition in *Notemigonus*. In all of the experiments reported here, body lipid reserves were higher in female fish exposed to the short photoperiod-low temperature regimes than in females maintained on long photoperiod-low temperature regimes. With the exception of the experiment conducted during the prespawning season, similar results were obtained with males. Short photoperiods also compliment the lipid depleting effects of warm temperatures. In two of the three experiments summarized here, body fat reserves were significantly lower in fish (both sexes) exposed to the short photoperiod-warm temperature regime than in animals maintained on the long photoperiod-warm temperature regime. Thus, in *Notemigonus*, the effects of photoperiod on lipid metabolism are temperature dependent. Specifically, in combination with a low temperature, short photoperiods favor body fat deposition, but at a high temperature, short photoperiods accelerate depletion of lipid reserves. The fact that short photoperiods have opposing effects on lipid metabolism depending on temperature is, at the present time, an enigma. Apparently, however, changing environmental temperatures can differentially sensitize *Notemigonus* to daylength. Roberts (1964) showed that photoperiod changes can alter metabolic patterns in sunfish. In *F. similis*, short photoperiods promote fattening whereas long photoperiods result in lipid depletion (de Vlaming, Sage, Charlton, and Tiegs; de Vlaming et al. in press). Other than these studies, little is known concerning the potential role of daylength in controlling fattening cycles in teleosts.

The results presented here on temperature and photoperiod effects on fat storage are consistent with environmental data. Lipid levels are lowest in *Notemigonus* collected during July, August and early September; environmental temperatures are high during this time and daylength is decreasing. From mid-September through December daylength and temperature continue to decrease. Fat stores increase progressively during this time. Beginning in mid or late February, lipid reserves are progressively depleted until late June or July. During this time, daylength and temperature are increasing.

A progressive decrease in body fat reserves was observed in *Notemigonus* collected during the preparatory, prespawning and spawning seasons respectively. These data indicate that there may be a relationship between lipid stores and reproduction. Other investigators presented evidence of body fat depletion associated with increasing gonadal activity (Lovern 1934; Lühmann 1953; Idler and Bitners 1960; Woodhead 1960; Wilkins 1967; Lasker 1970). A long photoperiod, in combination with warm temperatures, is required for final gonadal maturation and spawning in *Notemigonus* (de Vlaming 1975). These conditions result in depletion of fat stores in this species. The fat depleted from body storage sites could possibly be utilized for the energy demands of reproduction; in females, some of the body lipids may also be converted to yolk precursors and transported to the developing oocytes. So gonadal activation by long photoperiod-warm temperatures regimes may result in mobilization of body lipid reserves. Possibly, however, gonadal maturation may depend on the prior activation of lipid mobilization enzyme systems by long photoperiod-warm temperature regimes. The former hypothesis gains some support from observations of several investigators (e.g., Kobayashi 1953; Egami 1955; Oguro 1956) which indicate that sex steroids stimulate lipid synthesis in fishes. In vitro studies with *Notemigonus* liver preparations imply that estradiol-17β stimulates synthesis and transport of lipid by this tissue (Shing and de Vlaming unpubl. data). My intention is not to imply that only sex steroids are involved in regulation of lipid metabolism. Indeed, other hormones such as insulin (de Vlaming and Pardo 1975) and prolactin (see below) have distinct effects on fat metabolism in *Notemigonus*.

Low temperatures, regardless of photoperiod, maintain vitellogenesis and spermatocyte proliferation in *Notemigonus*, but will not stimulate final ovarian or testicular maturation (de Vlaming 1975). Low temperatures also maintain or increase body lipid reserves in this species. These observations lend further support to the suggestion that fat stores are in some way related to reproductive activity.

Short photoperiod-warm temperature regimes cause gonadal regression in *Notemigonus* (de Vlaming 1975). Body fat depletion also occurs under these conditions. Obviously this fat depletion is not associated with increased gametogenic activity. Body lipid reserves also decreased in fish maintained on long photoperiod-warm temperature regimes. Therefore, depletion of body fats may be primarily associated with increased energy requirements at high temperatures. In *Notemigonus*, however, there is some indication that sex steroid secretion is stimulated or remains high in fish maintained on a short photoperiod-warm temperature regime. Specifically, fish exposed to these conditions either develop or maintain nuptial coloration. If such is the case, sex steroids may be involved in mobilization and/or utilization of lipid reserves.

In a majority of the experiments reported here, pinealectomy had a pronounced effect on body fat reserves in *Notemigonus*. The effects of pinealectomy on fat metabolism depend on the photoperiod-temperature regime to which the experimental animals are exposed. In all three experiments, body lipid levels were significantly lower in pinealectomized than in sham operated females exposed to the long photoperiod-warm temperature regime; similar results were obtained with males in one experiment. Body lipid content was significantly greater in pinealectomized than in sham operated females in two of the three experiments where fish were exposed to a short photoperiod-warm temperature regime; similar results were obtained in only one experiment with males. These data indicate that, in fish maintained at warm temperatures, the effects of pinealectomy depend on photoperiod conditions. During the prespawning and spawning seasons, pinealectomy reversed the effects of photoperiod on fish exposed to a warm temperature. For example, lipid levels were not significantly different in pinealectomized fish exposed to the short photoperiod-warm temperature regime and sham operated animals maintained on the long photoperiod-warm temperature regime; nor was fat content significantly different in sham operated animals exposed to the short photoperiod-warm temperature condition and pinealectomized fish maintained on the long photoperiod-warm temperature regime (Tables 2, 3).

In all three of the experiments summarized here, body fat reserves were significantly greater in pinealectomized than in sham operated females maintained on the long photoperiod-low temperature regime; similar results were recorded in two of the experiments with males. Body fat composition was significantly lower in pinealectomized than in sham operated females exposed to a short photoperiod-low temperature regime; similar differences were noted with males in two of the experiments. These data further confirm the suggestion that the effects of pinealectomy on lipid metabolism in *Notemigonus* depend on photoperiod. In two of the experiments, fat content did not differ significantly in pinealectomized fish maintained on the long photoperiod-low temperature regime and sham operated animals exposed to the short photoperiod-low temperature regime; nor were significant differences noted in fat levels when the reverse comparison was made (Tables 2, 3).

The data obtained at both high and low temperatures indicate that the pineal in *Notemigonus* may have some role in receiving and/or integrating light information. Such a suggestion seems likely since the pineal may either facilitate or retard lipid deposition in this species. Several morphological and electrophysiological studies suggest that the pineal in some teleosts functions as a photoreceptor (cf. de Vlaming 1974). Light microscope studies on the pineal of *Notemigonus* also indicate a sensory function (Vodicnik and de Vlaming unpubl. data). If the pineal in *Notemigonus* is a photoreceptor involved by some means in measuring daylength, then removal of this organ from fish maintained under different photoregimes might be expected to have variable effects on lipid metabolism. Urasaki (1972a, b) has also shown that the effects of pinealectomy on reproductive function in *Oryzias latipes* vary with photoperiod conditions.

The effects of the pineal on lipid metabolism in *Notemigonus*, however, do not depend entirely on light information. For example, in fish maintained on a long photoperiod during the prespawning and spawning seasons, pinealectomy accentuated lipid deposition at low temperatures and lipid depletion at a high temperature. Temperature may not, however, act on the pineal directly. High temperatures cause lipid catabolism and low temperatures favor lipid deposition. Temperature may act directly on lipid metabolism enzyme systems or indirectly to stimulate hormone secretion from various endocrine glands. In *Notemigonus*, light information serves only to modify the effects of temperature on lipid metabolism. Thus, the pineal could function at all temperatures as a light receptor and/or integrator. Light information may be differentially interpreted (at different temperatures or at different times of the year) at some other level such as the hypothalamus and/or pituitary.

Whether the pineal in *Notemigonus* exerts its effects on lipid metabolism via neural or hormonal pathways is not presently known. Most morphological studies on the teleost pineal have stressed the dual sensory and secretory appearance of this organ (cf. de Vlaming 1974). A dual sensory-secretory function is also indicated by light microscope studies on the pineal of *Notemigonus*. Histochemical and biochemical data show that the teleost pineal has an active indolamine metabolism (Quay 1965; Hafeez and Quay 1969; Fenwick 1970; Owman and Rüdeberg 1970). Melatonin has inhibitory effects on reproductive function in various teleosts (Fenwick 1970; Urasaki 1972c; de Vlaming, Sage, and Charlton 1974). Melatonin treatment decreases lipid reserves in *F. similis* maintained on a long photoperiod-low temperature regime (de Vlaming, Sage, Charlton, and Tiegs 1974); if melatonin acts as the mediator of pineal action in *Notemigonus*, one might then expect pinealectomy to increase fat levels in fish exposed to a long photoperiod-low temperature regime. Pinealectomy did indeed have these results under this regime. During July, melatonin therapy of *F. similis* exposed to a short photoperiod-low temperature regime stimulated lipid deposition (de Vlaming, Sage, Charlton, and Tiegs 1974). If the mediator of pineal activity in *Notemigonus* is melatonin, one might predict that pinealectomy would decrease body lipid stores in animals exposed to a short photoperiod-low temperature regime. Such results were observed in the experiments reported here. Interestingly, lighting conditions were reported to alter the secretory activity in the glandular appearing pineals of *Gambusia affinis* and *Symphodus melops* (Chèze and Lahaye 1969; Chèze 1970). Possibly then, the pineal in some teleost species may function as a neuroendocrine transducer of photoperiod information. If the pineal is a neuroendocrine organ, melatonin could conceivably be one of the hormones produced by this organ. Although the pineal of *Notemigonus* does seem to be involved in photoreception, available evidence does not allow one to conclusively state that this organ is neuroendocrine in nature or that pineal-produced melatonin functions as a chemical messenger.

The pineal may modify fat stores in *Notemigonus* by influencing hypothalamic and/or pituitary function. Indeed, de Vlaming and Vodicnik (in press) showed that pinealectomy alters hypothalamic gonadotropin releasing activity and pituitary gonadotropin levels. Several investigators reported that prolactin has a pronounced affect on lipid metabolism in teleost fishes (Lee and Meier 1967; Meier 1969; Mehrle and Fleming 1970; Joseph and Meier 1971; Meier et al. 1971; de Vlaming and Sage 1972; Sage and de Vlaming 1973; de Vlaming et al. in press; Pardo and de Vlaming in press). Furthermore, melatonin treatment significantly reduces pituitary prolactin activity in *F. similis* (de Vlaming, Sage, Charlton, and Tiegs 1974). These authors suggested that the effects of melatonin on lipid metabolism in this species may be due in part to the effects of this indolamine on pituitary prolactin release. Whether pinealectomy alters pituitary prolactin secretion is not presently known. Investigations are presently in progress to examine this possibility. Prolactin does stimulate lipid depletion from in vitro liver preparations of *Notemigonus* incubated at high temperatures and promotes fat synthesis in liver preparations incubated at low temperatures (Pardo and de Vlaming in press).

The effects of pinealectomy on lipid reserves in *Notemigonus* may result from changes in reproductive activity. This suggestion seems rather unlikely since pinealectomy frequently resulted in significant changes in body fat levels without appreciably altering gonadal activity.

The data presented here favor the view that the pineal is a photoreceptor or integrates light information and plays an important role in regulating physiological processes in teleost fishes.

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LITERATURE CITED

BERGMANN, G.

1971. Electron microscopic studies of the pineal organ in *Pterophyllum scalare* Cuv. et Val. (Cichlidae, Teleostei). Z. Zellforsch. Mikrosk. Anat. 119:257-288.

BLAZKA, P.

1958. The anaerobic metabolism of fish. Physiol. Zool. 31:117-128.

BROWN, W. D.

1960. Glucose metabolism in carp. J. Cell. Physiol. 55:81-85.

CHÈZE, G.

1970. Étude morphologique, histologique, et expérimentale de l'épiphyse de *Symphodus melops* (Poisson, Labridaé). Bull. Soc. Zool. Fr. 94:697-704.

CHÈZE, G., AND J. LAHAYE.

1969. Etude morphologique de la région épiphysaire de *Gambusia affinis holbrooki G.* Incidences histologiques de certains facteurs externes sur le toit diencéphalique. Ann. Endocrinol. 30:45-53.

DEAN, J. M., AND C. J. GOODNIGHT.

1964. A comparative study of carbohydrate metabolism in fish as affected by temperature and exercise. Physiol. Zool. 37:280-299.

DE VLAMING, V. L.

1971. The effects of food deprivation and salinity changes on reproductive function in the estuarine gobiid fish, *Gillichthys mirabilis*. Biol. Bull. (Woods Hole) 141:458-471.

1972. Environmental control of teleost reproductive cycles: A brief review. J. Fish Biol. 4:131-140.

1974. Environmental and endocrine control of teleost reproduction. *In* C. B. Schreck, Control of sex in fishes, p. 13-83. Sea Grant and V.P.I. & S.U. Press, V.P.I.-S.G.-74-01.

1975. Effects of pinealectomy on gonadal activity in the cyprinid teleost, *Notemigonus crysoleucas*. Gen. Comp. Endocrinol. 26:36-49.

DE VLAMING, V. L., AND R. J. PARDO.

1975. *In vitro* effects of insulin on liver carbohydrate and lipid metabolism in the cyprinid teleost, *Notemigonus crysoleucas*. Comp. Biochem. Physiol. 51B:489-497.

DE VLAMING, V. L., AND M. SAGE.

1972. Diurnal variation in fattening response to prolactin treatment in two Cyprinodontid fishes, *Cyprinodon variegatus* and *Fundulus similis*. Contrib. Mar. Sci., Univ. Tex. 16:59-63.

DE VLAMING, V. L., M. SAGE, AND C. B. CHARLTON.

1974. The effects of melatonin treatment on gonosomatic index in the teleost, *Fundulus similis*, and the tree frog, *Hyla cinerea*. Gen. Comp. Endrocrinol. 22:433-438.

DE VLAMING, V. L., M. SAGE, C. B. CHARLTON, AND B. TIEGS.

1974. The effects of melatonin on lipid deposition in cyprinodontid fishes and on pituitary prolactin activity in *Fundulus similis*. J. Comp. Physiol. 94:309-319.

de Vlaming, V. L., M. Sage, and R. Tiegs.
In press. A diurnal rhythm of pituitary prolactin activity with diurnal effects of mammalian and teleostean prolactin on total body lipid deposition and liver lipid metabolism in teleost fishes. J. Fish Biol.

de Vlaming, V. L., and M. J. Vodicnik.
In press. Effects of pinealectomy on pituitary gonadotropin potency and hypothalamic gonadotropin releasing activity in the cyprinid teleost, *Notemigonus crysoleucas.* J. Fish Biol.

Egami, N.
1955. Effect of estrogen and androgen on the weight and structure of the liver of the fish, *Oryzias latipes.* Annot. Zool. Jap. 28:79-85.

Fenwick, J. C.
1970. Demonstration and effect of melatonin in fish. Gen. Comp. Endocrinol. 14:86-97.

Hafeez, M. A.
1971. Light microscopic studies on the pineal organ in teleost fishes with special regard to its function. J. Morphol. 134:281-314.

Hafeez, M. A., and W. B. Quay.
1969. Histochemical and experimental studies of 5-hydroxytryptamine in pineal organs of teleosts (*Salmo gairdneri* and *Atherinopsis californiensis*). Gen. Comp. Endocrinol. 13:211-217.
1970. Pineal acetylserotonin methyltransferase activity in the teleost fishes, *Hesperoleucas symmetricus* and *Salmo gairdneri* with evidence for lack of effect of constant light and darkness. Comp. Gen. Pharmacol. 1:257-262.

Hochachka, P. W.
1969. Intermediary metabolism in fishes. *In* W. S. Hoar and D. J. Randall, (editors), Fish physiology, Vol. 1, p. 351-389. Academic Press, N.Y.

Idler, D. R., and I. Bitners.
1960. Biochemical studies on sockeye salmon during spawning migration. IX. Fat, protein and water in the major internal organs and cholesterol in the liver and gonads of the standard fish. J. Fish. Res. Board Can. 17:113-122.

Joseph, M. M., and A. H. Meier.
1971. Daily variations in the fattening response to prolactin in *Fundulus grandis* held on different photoperiods. J. Exp. Zool. 178:59-62.

Kinne, O.
1960. Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiol. Zool. 33:288-317.

Knipprath, W. C., and J. F. Mead.
1968. The effect of the environmental temperature on the fatty acid composition and on the *in vivo* incorporation of 1-^{14}C-acetate in goldfish (*Carassius auratus* L.). Lipids 3:121-128.

Kobayashi, H.
1953. Effects of estrone upon the structure, weight and fat content of the liver in the fish, *Misgurnus anguillicaudatus.* Annot. Zool. Jap. 26:213-216.

Lasker, R.
1970. Utilization of zooplankton energy by a Pacific sardine population in the California current. *In* J. H. Steele (editor), Marine food chains, p. 265-284. Univ. Calif. Press, Berkeley.

Lee, R. W., and A. H. Meier.
1967. Diurnal variations of the fattening response to prolactin in the golden topminnow, *Fundulus chrysotus.* J. Exp. Zool. 166:307-316.

Love, R. M.
1957. The biochemical composition of fish. *In* M. E. Brown (editor), The physiology of fishes, Vol. I, Metabolism, p. 401-418. Academic Press, N.Y.

Lovern, J. A.
1934. Fat metabolism in fishes. IV. Mobilisation of depôt fat in the salmon. Biochem. J. 28:1955-1960.

Lühmann, M.
1953. Uber die Fettspeicherung bei Ostseeheringen und ihre Beziehung zum Fortpflanzungszyklus. Kiel Meeresforsch. 9:213-227.

Mehrle, P. M., and W. R. Fleming.
1970. The effect of early and midday prolactin injection on the lipid content of *Fundulus kansae* held on a constant photoperiod. Comp. Biochem. Physiol. 36:597-603.

Meier, A. H.
1969. Diurnal variations of metabolic responses to prolactin in lower vertebrates. Gen. Comp. Endocrinol. Suppl. 2:55-62.

Meier, A. H., T. N. Trobec, M. M. Joseph, and T. M. John.
1971. Temporal synergism of prolactin and adrenal steroids in the regulation of fat stores. Proc. Soc. Exp. Biol. Med. 137:408-415.

Nikolsky, G. V.
1963. The ecology of fishes. Academic Press, N.Y.

Oguro, C.
1956. Some observations on the effect of estrogen upon the liver of the three-spined stickleback, *Gasterosteus aculeatus aculeatus* L. Annot. Zool. Jap 29:19-22.

Oksche, A. M., M. Ueck, and C. Rüdeberg.
1971. Comparative ultrastructural studies of sensory and secretory elements in pineal organs. Mem. Soc. Endocrinol. 19:7-25.

Omura, Y., and M. Oguri.
1969. Histological studies on the pineal organ of 15 species of teleosts. Bull. Jap. Soc. Sci. Fish. 35:991-1000.

Owman, C., and C. Rüdeberg.
1970. Light, fluorescence, and electron microscopic studies on the pineal organ of the pike, *Esox lucius* L., with special regard to 5-hydroxytryptamine. Z. Zellforsch. Mikrosk. Anat. 107:522-550.

Pardo, R. J., and V. L. de Vlaming.
In press. *In vivo* and *in vitro* effects of prolactin on lipid metabolism in the cyprinid teleost, *Notemigonus crysoleucas.* Copeia.

Quay, W. B.
1965. Retinal and pineal hydroxyindole-O-methyl transferase activity in vertebrates. Life Sci. 4:983-991.

Reiter, R. J.
1973. Comparative physiology: Pineal gland. Ann. Rev. Physiol. 35:305-328.

Rizkalla, W.
1970. The morphology of the pineal organ in the teleost, *Clarias lazera* C. V. Acta Biol. Acad. Sci. Hung. 21:25-35.

Roberts, J. L.
1964. Metabolic responses of fresh-water sunfish to seasonal photoperiods and temperatures. Helgoländer wiss. Meeresunters. 9:459-473.

RÜDEBERG, C.

1966. Electronmicroscopic observations on the pineal organ of the teleosts *Mugil auratus* (Risso) and *Uranoscopus scaber*. Pubbl. Stn. Zool. Napoli 35:47-60.

1969. Structure of the parapineal organ of the adult rainbow trout, *Salmo gairdneri* Richardson. Z. Zellforsch. Mikrosk. Anat. 93:282-304.

SAGE, M., AND V. L. DE VLAMING.

1973. A diurnal rhythm in hormone effectiveness and in pituitary content of prolactin in *Fundulus similis*. Tex. Rep. Biol. Med. 31:101-102.

TAKAHASHI, H.

1969. Light and electron microscope studies on the pineal organ of the goldfish, *Carassius auratus* L. Bull. Fac. Fish., Hokkaido Univ. 20:143-157.

URASAKI, H.

1972a. Effect of pinealectomy on gonadal development in the Japanese killifish (Medaka), *Oryzias latipes*. Annot. Zool. Jap. 45:10-15.

1972b. Role of the pineal gland in gonadal development in the fish, *Orzyias latipes*. Annot. Zool. Jap. 45:152-158.

1972c. Effects of restricted photoperiod and melatonin administration on gonadal weight in Japanese killifish. J Endocrinol. 55:619-620.

WILKINS, N. P.

1967. Starvation of the herring, *Clupea harengus* L.: Survival and some gross biochemical changes. Comp. Biochem. Physiol. 23:503-518.

WOODHEAD, A. D.

1960. Nutrition and reproductive capacity in fish. Proc. Nutr. Soc. 19:23-28.

RELATIONSHIPS BETWEEN ZOOPLANKTON DISPLACEMENT VOLUME, WET WEIGHT, DRY WEIGHT, AND CARBON[1]

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ABSTRACT

Interconversion of various measures of zooplankton biomass have great utility in studies requiring nondestructive techniques, or for interpretation of past data. In establishing predictive relationships between such measures, the appropriate regression to use is the geometric mean estimate, which provides a regression line in which the regressions of X on Y and Y on X are identical. We have employed this type of analysis in determinations on samples from diverse sea areas in different seasons and have determined that statistically significant relationships exist between carbon, wet weight, displacement volume, and dry weight when a constant technique is used. The slope of the regression line for log transformed values for carbon vs. dry weight and wet weight vs. displacement volume was sufficiently close to unity to assume a straight percentage conversion between these values. Carbon was 31-33% of dry weight and wet weight was 72-73% of displacement volume, according to our techniques. Comparability of different techniques for a biomass measurement may be poor, especially in the case of displacement volume and wet weight measurements due to variations in the interstitial water content. Moreover, interstitial water content varies inversely with total biomass density, which accounts for the absence of a simple percentage relationship between wet weight or displacement volume and other measures of zooplankton biomass.

Biomass is a classic and useful measure of the zooplankton standing crop. A number of techniques exist to measure it. Four commonly used techniques involve measurement of displacement volume (Yentsch and Hebard 1957; Frolander 1957; Sutcliffe 1957; Tranter 1960; Ahlstrom and Thrailkill 1963), wet weight (Nakai and Honjo 1962), dry weight (Lovegrove 1966), and carbon (Curl 1962; Platt et al. 1969). For most studies, especially those determining energy flow through food chains, carbon is the most fundamental of these gross measures. Many zooplankton collections frequently serve several purposes and the destructive techniques required to determine carbon or dry weight frequently cannot be employed. An alternative is to measure displacement volume or wet weight, and convert the data into either dry weight or carbon. These latter techniques, if done properly, are nondestructive since the organisms can still be identified when re-suspended in liquid. There is an obvious need for conversion factors that reliably define the relationship between the various biomass measures. This need also arises when data based on different techniques are compared. Although conversion factors exist in the literature, they often are based on data from restricted sea areas. Further, in some cases, biomass determinations were made by techniques which are no longer recommended (see Lovegrove 1966). The objective of this paper is to more satisfactorily define the relationships between the biomass measures mentioned above. Using both data derived from samples collected from diverse oceanic areas over the past 6 yr and data selected from the literature, we have empirically determined linear regression equations relating pairs of biomass measures.

THEORETICAL CONSIDERATIONS

Ideally, any two biomass measures, X and Y should be related by a constant of proportionality, a, such that

$$Y = a\,X^{\beta}, \tag{1}$$

where $\beta = 1.0$. A measurement error or bias which occurs as a constant fraction of the biomass results only in a change in the value of a. When natural variability or an error factor(s) in X or Y is disproportionate or inversely proportional to the amount of biomass, β cannot be assumed to equal

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1.0 and Y is not a simple percentage of X. If β is a constant, then the $\log_{10}$ of the two measures will be linearly related:

$$\mathrm{Log}_{10}(Y) = \mathrm{Log}_{10}(a) + \beta \, \mathrm{Log}_{10}(X). \qquad (2)$$

In the sections which follow, we will show that in most cases $\beta \neq 1.0$ and equation (2) is adequate for describing the linear relationship between log transformed measures of biomass.

METHODS

The station locations where samples were collected are shown in Figure 1 (symbol key given in Table 1). At many of these stations, more than one sample was collected. A single symbol may represent a number of collections as indicated in Table 1. Not shown are the stations of *Gosnold* 140, a cruise to the coastal upwelling region off Peru.

Collections were made with 70-cm or 100-cm diameter ring nets, 70-cm diameter Bongo nets (McGowan and Brown 1966), or the 50 × 50 cm net (Bé et al. 1971), all equipped with a flowmeter (Table 1). In shallow regions, Buzzards Bay, *Atlantis II* 52 (continental Atlantic shelf), *Gosnold* 140 (Peru Current), *Gosnold* 166 (New York Bight), tows were made to near the bottom. In deeper waters, oblique tows were generally made to below 300 m.

Ring net collections were generally split with a plankton splitter (McEwen et al. 1954). One-half was preserved in 10% buffered Formalin[1] for displacement volume analysis and the other half was frozen in a chest freezer for wet weight, dry weight, and carbon analyses (re Bermuda Table 1: Menzel and Ryther (1961) do not state how this half was stored prior to analysis). A similar procedure was carried out for Bongo net collections; one of the paired samples was preserved in Formalin while the other was frozen.

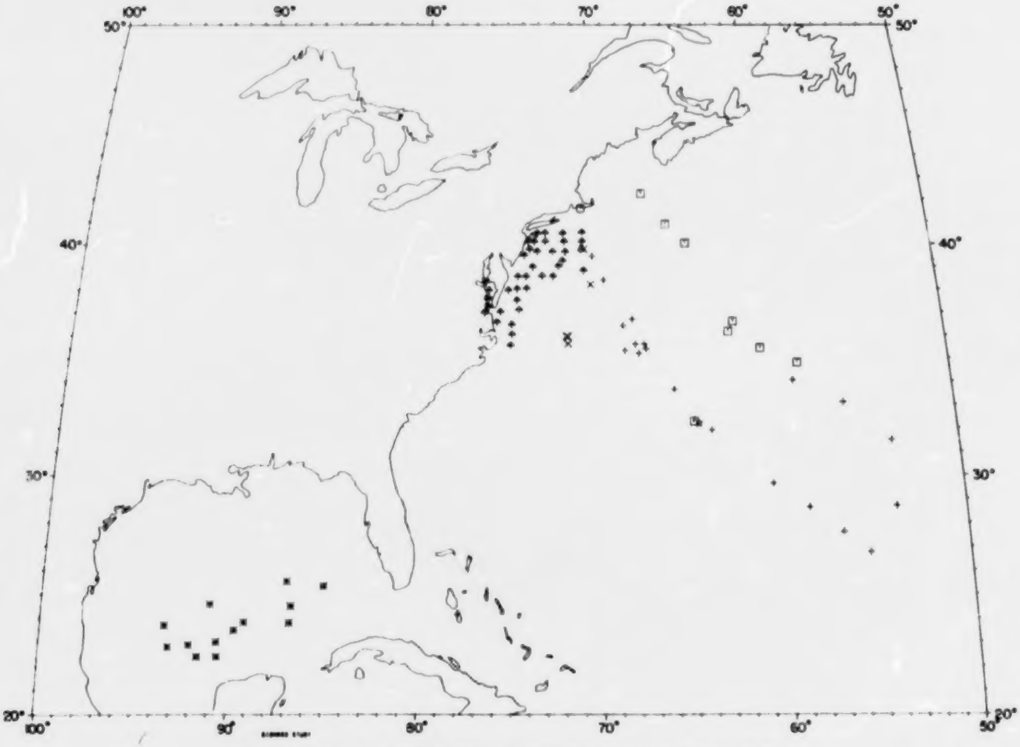

FIGURE 1.–Location of zooplankton collection sites. For symbols, see Table 1.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.–Number of observations and symbol designation for each cruise or area from which zooplankton samples were collected. The symbols are used in Figures 1 and 3-5.

			Number of observations				
Cruise or area	Symbol	Date(s)	Displacement volume	Wet weight	Dry weight	Carbon	Type of net (mesh)
Buzzards Bay	○	Jan.-June 1972	15	16	16	16	70 cm (240 µm) diam.
Slope	△	June-Aug. 1972	14	12	14	14	100 cm (333 µm) diam.
Bermuda[1]	☆	1957-59	52	0	52	0	100 cm (366 µm) diam.
Gosnold 140	⌑	May 1969	[2]0	0	33	33	70 cm (240 µm) diam.
Gosnold 166	⬠	June 1970	32	0	33	33	70 cm (240 µm) diam.
Atlantis II 48	✱	Nov. 1968	0	0	20	20	70 cm (240 µm) diam.
Atlantis II 52	▲	Sept. 1969	0	0	37	37	70-cm (240 µm) diam. Bongos
Atlantis II 71	+	Sept. 1972	27	43	43	42	100 cm (333 µm) diam.
Chain 111	□	Feb. 1973	13	13	13	0	100 cm (333 µm) 70-cm Bongos
Knorr 35 II	×	Nov. 1973	10	11	11	0	100 cm (333 µm) 70-cm Bongos
Bé North Atlantic	◇	—[3]	229	229	229	0	50 × 50 cm (202 µm)
Bé South Atlantic	+	—[4]	176	192	193	0	50 × 50 cm (202 µm)

[1] Data from Menzel and Ryther (1961).
[2] Omitted, bad data.
[3] See Bé et al (1971) for geographical and seasonal coverage.
[4] Data from Bé (footnote 5).

Displacement volumes were measured by one of two techniques. The Mercury Immersion method of Yentsch and Hebard (1957) was used to determine the values given by Menzel and Ryther (1961-Bermuda), by Bé et al. (1971-North Atlantic) and Bé (1973-unpubl. data for the South Atlantic).[5] A modified version of the Mercury Immersion technique was used to measure displacement volumes on *Gosnold* 140, but further work has shown that the method has significant variable errors and is unreliable (Grice and Wiebe unpubl. data). We have not, therefore, used the *Gosnold* 140 displacement volume data. All other displacement volumes were measured by the method described by Ahlstrom and Thrailkill (1963) after removal of all organisms larger than 5 cc. For split samples, organisms larger than 5 cc were removed prior to the split. On *Gosnold* 166, displacement volumes were run prior to sample preservation (see Vaccaro et al. 1972 for data) and again 2 yr after preservation. Contrary to the findings of Ahlstrom and Thrailkill (1963), shrinkage did not occur (Figure 2). These samples were, however, heavily dominated by copepods (Wiebe et al. 1973) which are least likely to undergo shrinking.

Wet weight was measured by straining the plankton through a 333-µm plankton gauze, rinsing with freshwater, and blotting the remaining mass on absorbant paper towels until water was no longer absorbed onto the towel. The biomass was then transferred to a pre-weighed glass jar with a stainless steel spatula. The jar was weighed on a Mettler balance to ± 2.5 mg and the wet weight of plankton determined by subtracting the jar weight from the total. Each jar was then dried to constant weight in an oven at 60°C. This

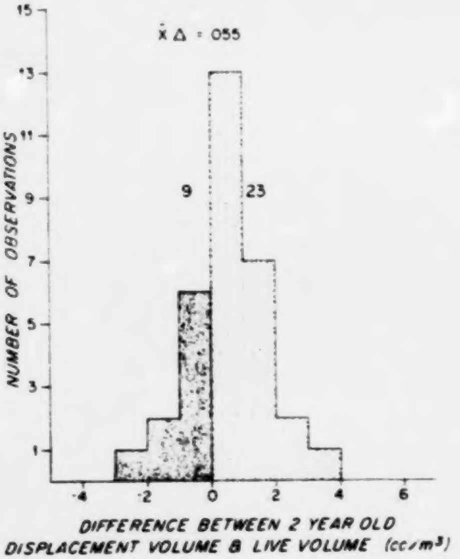

FIGURE 2.–Distribution of differences between displacement volumes measured 2 yr after preservation and the live displacement volume. The live displacement volumes ranged from 30 to 321 cc (0.57 to 2.53 cc/m³) and the 2-yr values ranged from 38 to 340 cc (0.58-2.40 cc/m³).

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[5] Bé, A. W. H. 1973. Studies of zooplankton standing stock in the South Atlantic. Unpubl. final tech. rep. to Natl. Sci. Found., 14 p.

frequently took 2 wk or longer owing to the large volumes of plankton collected. Dried samples were pulverized and an aliquot(s) of the powder used to determined carbon in either a Perkin-Elmer No. 240 or a Hewlett Packard No. 185 B carbon, hydrogen, nitrogen analyzer. A number of exceptions to this procedure are evident in Table 1. In some cases, wet weight was not measured; in others, carbon was not determined.

All data presented below were standardized to biomass per cubic meter and then logarithmically transformed (base 10) before use in the regression analyses.

RESULTS

Several regression lines can be used to express the relationship between pairs of variables (Ricker 1973). The appropriate one is determined by the frequency distribution of the parent population as well as the nature of the error sources in the measurements (natural or measurement error). Since the biomass measures are all subject to natural variability and measurement error and since the observations presented cannot be assumed to be a random sample from a bivariate normal population, the "geometric mean (GM) estimate of the functional regression of Y on X" (Ricker 1973:412) is appropriate. As Ricker points out, this regression line minimizes the sum of the products of the vertical and horizontal distance of each point from the line. Thus, the GM regression lines of Y on X and X on Y are identical. Given the GM regression equation:

$$Y' = u + vX', \tag{3}$$

where $Y' = \log(Y)$ and $X' = \log(X)$, one can determine both an X given Y or Y given X. Although Ricker's (1973) paper should be consulted for an in depth discussion of the assumptions and computations, we note that the slope, v, is given by:

$$v = \pm\frac{b}{r} = \pm\sqrt{\frac{\Sigma(y_i'-\overline{Y}')^2}{\Sigma(x_i'-\overline{X}')^2}}, \tag{4}$$

where b is the slope of the predictive regression of Y' on X' and r is the correlation coefficient. The Y'-axis intercept, u, is easily determined by:

$$u = \overline{Y}' - v\overline{X}'. \tag{5}$$

Plots of the values used in the GM regressions are given in Figures 3-5. The equations are listed in Table 2. All equations have slopes significantly different from zero ($P<0.001$). As indicated above, in the case where β of Equation (1) (v of Equation (3)) is equal to 1.0, one biomass measure is a straight percentage of another. The only regressions with a v approaching 1.0 compare dry weight to carbon and displacement volume to wet weight. In these cases, predicted carbon varies from 31 to 33% of zooplankton dry weight and predicted wet weight varies from 72 to 73% of displacement volume. In all other regressions, a variable bias is present which causes v to deviate from 1.0. We believe that a large portion of the bias is caused by the interstitial water present in displacement volumes and wet weights. This bias is inversely proportional to the sample size; i.e., a small sample

TABLE 2.–Functional (geometric mean) regression equations for pairs of biomass measures. Carbon: C; dry weight: DW; wet weight: WW; displacement volume: DV; Bé et al. (1971) and Bé (footnote 5) wet weight: BWW; Bé et al. (1971) and Bé (footnote 5) displacement volume: BDV; Bé et al. (1971) and Bé (footnote 5) dry weight: BDW; Platt et al. (1969) dry weight: PDW; Platt et al. (1969) carbon: PC. Logarithms to the base 10.

Equation	Regression equation	N	Variance of slope	r^2
1	Log (DV) = −1.429 + 0.808 Log(C)	87	0.0003187	0.96
2	Log(WW) = −1.537 + 0.822 Log(C)	70	0.0008303	0.92
3	Log(DW) = 0.508 + 0.977 Log(C)	193	0.0001438	0.97
4	Log(DV) = −1.828 + 0.848 Log(DW)	161	0.0001814	0.96
5	Log(WW) = −1.983 + 0.922 Log(DW)	93	0.0005800	0.94
6	Log(DV) = 0.670 + 0.950 Log(WW)	77	0.0013729	0.90
7	Log(BWW) = −1.897 + 0.835 Log(BDW)	420	0.0009725	0.63
8	Log(BDV) = −1.826 + 0.754 Log(BDW)	404	0.0011106	0.56
9	Log(BDV) = −0.219 + 0.848 Log(BWW)	403	0.0006079	0.75
10	Log(PDW) = 0.558 + 1.024 Log(PC)	45	0.0148049	0.39
11	Log(DV)[1] = 1.048 + 0.821 Log(DW)	110	0.0010510	0.83
12	Log(WW)[1] = 0.975 + 0.946 Log(DW)	94	0.0010173	0.90
13	Log(DV)[1] = 0.078 + 1.026 Log(WW)	75	0.0022271	0.85

[1] Note that biomass data used to determine equations 1-10 were standardized to per cubic meter while the data used to determine equations 11-13 were not standardized.

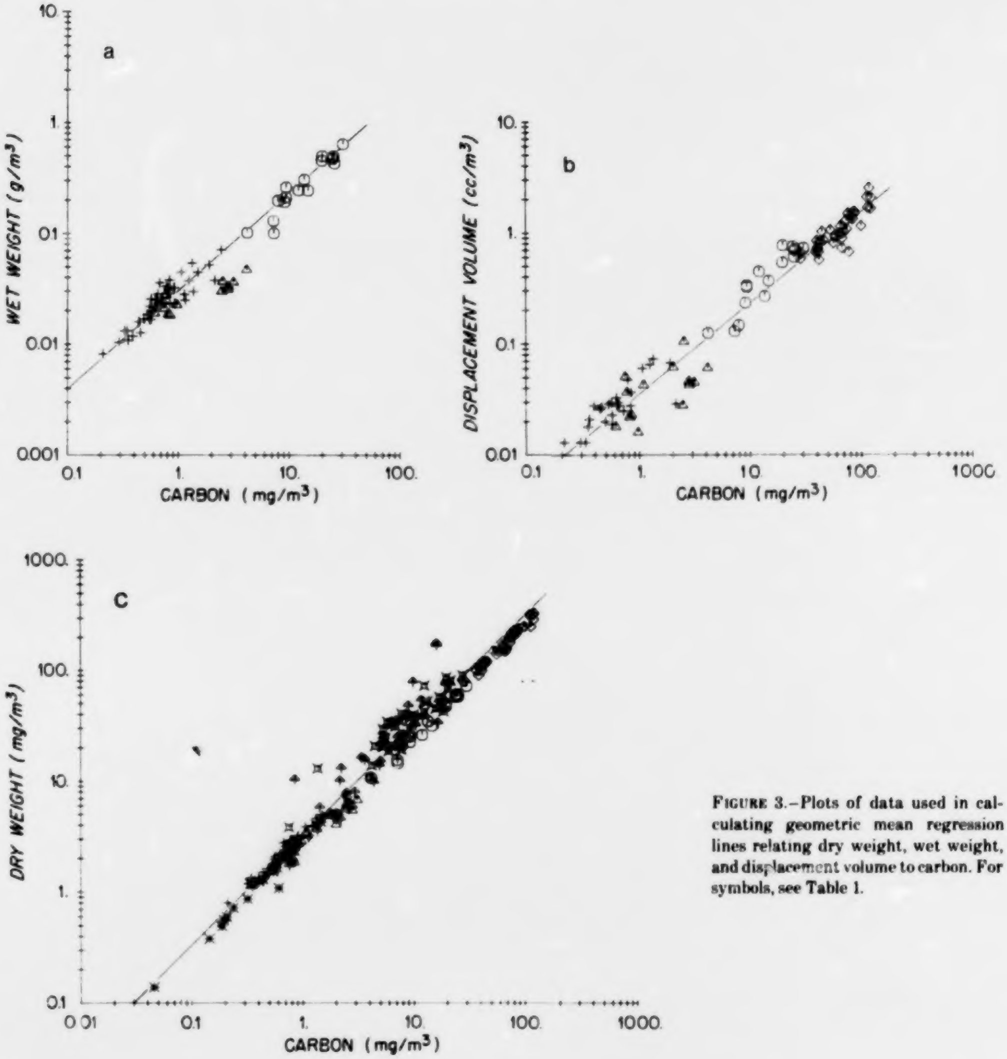

FIGURE 3.—Plots of data used in calculating geometric mean regression lines relating dry weight, wet weight, and displacement volume to carbon. For symbols, see Table 1.

appears to have a larger percentage of interstitial water than a large sample. It is evident in our log transformed raw data as well as the data standardized to biomass per cubic meter and then log transformed (see Table 4). The reason why the bias is not significantly influenced by the standardization to biomass per cubic meter results from the fact that the volume of water filtered in collecting most samples was quite similar, between 100 and 1,000 m^3, while the biomass per cubic meter varied by as much as four orders of magnitude. As a result of the variable bias, it is not valid to assume a simple percentage relationship between the other pairs of biomass estimators. For example, dry weight is approximately 5% of displacement volume for low biomass per cubic meter and approximately 13% for high biomass per cubic meter.

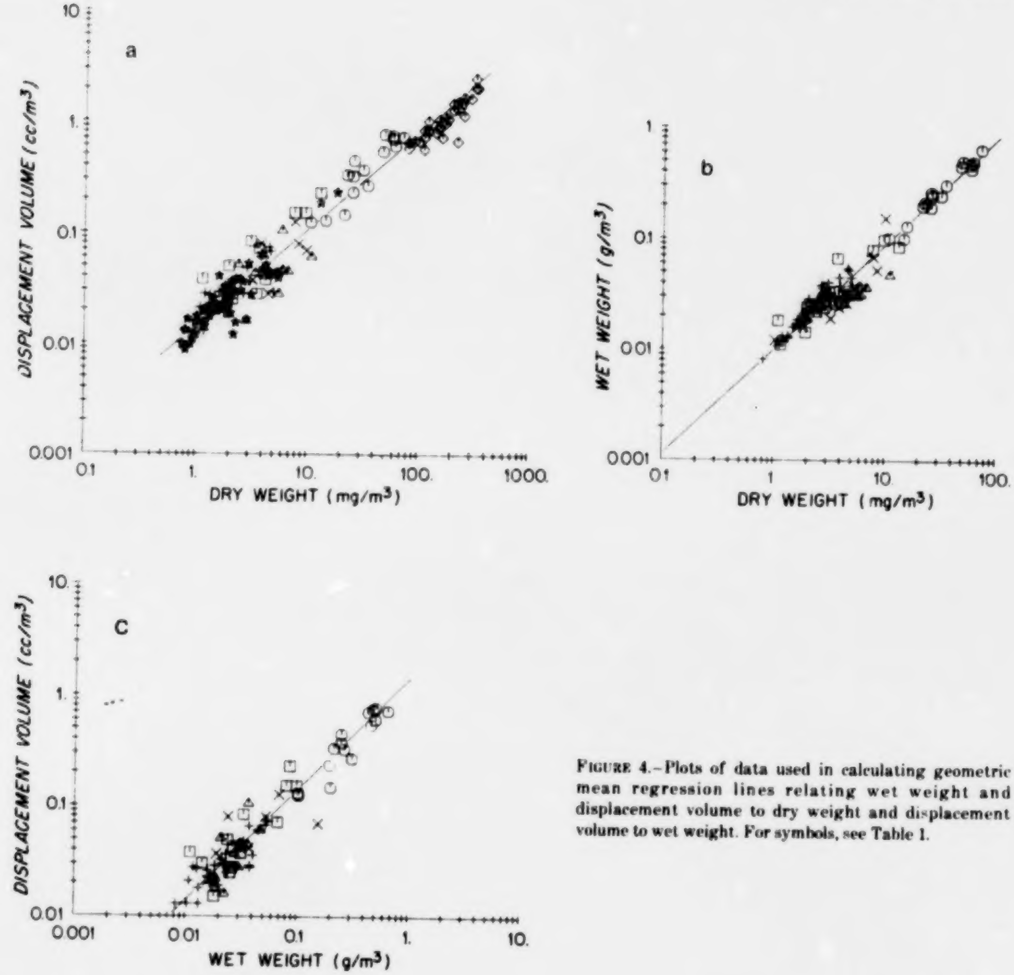

FIGURE 4.–Plots of data used in calculating geometric mean regression lines relating wet weight and displacement volume to dry weight and displacement volume to wet weight. For symbols, see Table 1.

Confidence limits can be calculated for predicted values of X or Y. Following Ricker (1973:411), the general form of the variance estimate for a single estimate of Y' given X' is:

$$S_{y'x'}^2\left(1 + \frac{1}{N} + \frac{(P_{x'} - \overline{X}')^2}{SSX'}\right), \qquad (6)$$

where $S_{y'x'}^2$ is the variance of observations from the regression line in the vertical direction, N is the number of observation pairs in the regression, and $P_{x'}$ is the value of X' used to estimate Y'. In the reverse case where X' is being predicted, $S_{x'y'}^2$, SSY', $P_{y'}$, and $\overline{Y}'$ are substituted for $S_{y'x'}^2$, SSX', $P_{x'}$, and $\overline{X}'$. Because we have used GM regression equations rather than predictive regression equations, the use of Expression (6) is not strictly legitimate. However, Ricker (1973:413) finds the error involved is small and concludes that "... it is possible to recommend using ordinary symmetrical confidence limits for the GM regression. They are a reasonable approximation to the true limits and will rarely lead to incorrect conclusions."

The values required to use Expression (6) to calculate confidence limits for predicted X's or Y's are given in Table 3. This variance and the t_{95} value are used to construct confidence limits for the logarithms:

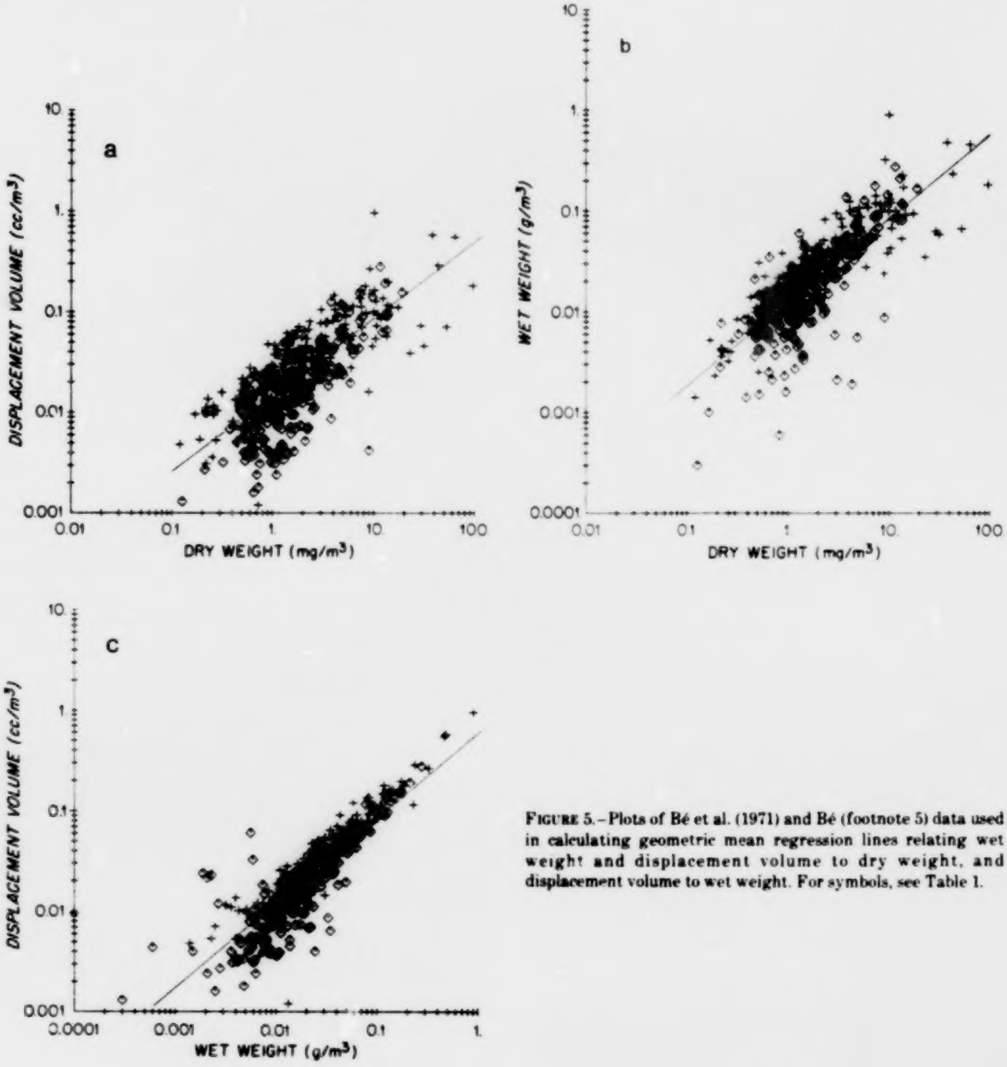

FIGURE 5.–Plots of Bé et al. (1971) and Bé (footnote 5) data used in calculating geometric mean regression lines relating wet weight and displacement volume to dry weight, and displacement volume to wet weight. For symbols, see Table 1.

$$Y' \pm t_{95}\sqrt{\hat{V}\mathrm{ar}\, Y'} \text{ or } X' \pm t_{95}\sqrt{\hat{V}\mathrm{ar}\, X'}.$$

Antilogging provides multiplicative limits for the untransformed data. For example, suppose an estimate of carbon is desired having measured a displacement volume (Y) of 0.1 cc/m³. Using Equation 1 in Table 2 and Expression (6) the following values result:

Log (Y)	*Log* (X)	X(mg/m³)	*Log (upper limit)*	*Upper limit*	*Log (lower limit)*	*Lower limit*
-1.0	0.557	3.61	0.916	8.25	0.198	1.58

Thus, the antilogged estimate of carbon is 3.6% of the displacement volume with upper and lower 95% limits of 8.3% and 1.6%.

Comparison of the regressions based upon the data of Bé et al. (1971) and Bé (footnote 5) with the

TABLE 3.–Values required to calculate 95% limits for values of X or Y predicted from regression equations in Table 2. The t_{95} value is based on the number of observations for each regression. For comparison abbreviations see Table 2 caption.

Comparison	t_{95}	Prediction of Y: $\bar{X}$	Prediction of Y: SSX	Prediction of Y: S_{yx}^2	Prediction of X: $\bar{Y}$	Prediction of X: SSY	Prediction of X: S_{xy}^2
DV vs. C	1.98	0.8310	69.3796	0.022095	−0.7573	47.1915	0.032483
WW vs. C	2.00	0.2076	22.0394	0.018282	−1.3663	16.1224	0.024992
DW vs. C	1.96	0.6456	117.7726	0.016987	1.1383	115.5700	0.017311
DV vs. DW	1.96	0.8369	106.4068	0.019299	−1.1181	79.6486	0.025782
WW vs. DW	1.98	0.6473	19.9736	0.011558	−1.3868	18.0252	0.012808
DV vs. WW	1.99	−1.3706	17.3509	0.023822	−1.2347	17.4390	0.023701
BDV vs. BDW	1.96	0.2408	85.9032	0.093843	−1.6446	63.8768	0.092518
BWW vs. BDW	1.96	0.2343	87.7505	0.085121	−1.7010	73.2612	0.077210
BDV vs. BWW	1.96	−1.6813	89.1699	0.054240	−1.6439	65.8228	0.056355
PDW vs. PC	2.02	0.6992	1.9394	0.028706	1.5742	2.0334	0.027378
DV vs. DW[1]	1.99	0.3918	25.6916	0.026995	1.3693	17.3094	0.040067
WW vs. DW[1]	1.99	0.1432	10.9063	0.011083	1.1101	9.7621	0.012383
WW vs. DV[1]	1.99	1.0998	7.1279	0.015876	1.2063	7.5091	0.015070

[1] Calculated values based on biomass data which was not standardized to per cubic meter.

regressions based solely on our data reveals two notable features. First, the slopes of the regressions based on the same biomass estimators; i.e., displacement volume versus dry weight, wet weight versus dry weight, and displacement volume versus wet weight, are significantly different ($P<0.05$). This was tested by calculating approximately 95% limits for the difference in slopes using standard normal distribution theory: $(r_w - r_{\text{Bé}}) \pm 1.96\sqrt{\hat{V}\text{ar}\, r_w + \hat{V}\text{ar}\, r_{\text{Bé}}}$. As was true in our cases, if $\Delta r \pm 95\%$ limit does not cross 0, the slopes are significantly different. In all cases, slopes of the regressions derived from our data are closer to 1.0.

The second feature is that there is a significant difference ($P<0.005$) in the variance of observations from the regression lines. The Bé et al. (1971) and Bé (footnote 5) variance for displacement volume versus dry weight is 4.9 times larger than that calculated for our data; for wet weight versus dry weight, it is 7.4 times larger; for displacement volume versus wet weight it is 2.3 times larger.

These differences are probably due in large part to the differences in methods used to determine displacement volume and wet weight. The mercury immersion method Bé et al. (1971) and Bé (footnote 5) used to measure displacement volume provides estimates substantially more variable than the technique used by us (Grice and Wiebe unpubl. data). The increased variability of their wet weights may have resulted from their use of a vacuum to remove some of the interstitial water.

One implication of the lower slopes for the Bé et al. (1971) and Bé (footnote 5) data is that it appears the percentage of interstitial water in their samples may change more radically with increasing biomass than in our samples. This inference is drawn from the calculated values relating dry weight to wet weight and displacement volume in percent (Table 4). The alternate explanation is that as biomass per cubic meter increases, the percentage of wet weight or displacement volume that constitutes dry weight increases as a result of a decrease in intracellular water. It seems unlikely that this accounts for the differences between the two sets of data. Seasonal effects have been minimized by collection of samples at various times of the year and geographical effects should be similar since both studies covered wide geographical ranges.

TABLE 4.–Regression equation prediction of the percentage of displacement volume (DV) or wet weight (WW) that is dry weight (DW) for selected dry weight concentrations.

DW (mg/m³)	Bé et al. (1971) and Bé (footnote 5): % DV	Bé et al. (1971) and Bé (footnote 5): % WW	This study: % DV	This study: % WW	DW[1] (g)	This study: % DV	This study: % WW
0.1	3.80	5.39	5.10	8.95	0.1	5.9	9.4
1.0	6.70	7.89	6.95	10.95	1.0	9.0	10.6
10.0	11.80	11.53	9.48	11.27	10.0	13.5	12.0
100.0	20.80	16.87	12.94	12.65	100.0	20.5	13.6

[1] Calculated values based on biomass data which were not standardized to per cubic meter.

DISCUSSION

Platt et al. (1969), in a comparison of the seasonal changes in dry weight, carbon, and caloric values of zooplankton collected from St. Margaret's Bay, Nova Scotia, found a fivefold variation in caloric content per unit dry weight. As a result they concluded ". . . that there is no single conversion factor that will serve to convert biomass of zooplankton, expressed as dry weight, to its energy equivalent." A similar conclusion was inferred for the conversion of dry weight to carbon. They found, however, that the carbon content of zooplankton could be used to predict the energy equivalent. These results appear to contradict our finding that a statistically significant relationship does exist between pairs of the different measures of biomass including dry weight and carbon. The explanation for this discrepancy lies in the fact that the data of Platt et al. represents a small segment of the extensive range of biomass per cubic meter which occurs in marine waters. This fact, coupled with high variation of the dry weight to carbon ratios, appeared to them to provide a nonsignificant relationship. We have used their data (as tabulated by Platt and Irwin 1968, table 4) to examine the fit of their data to our regression line. After transformation to logarithms (base 10), a linear GM regression line was calculated for their 45 pairs of dry weight and carbon values. While the slope of this line was significantly different from zero ($P<0.001$), it was nonsignificantly different ($P>0.05$) from ours (Table 2). However, the intercept was substantially different. This is a reflection of the fact that their carbon values average 14% of dry weight, whereas in our data the average is 32%. The wet-combustion method (described by Strickland and Parsons 1965) which they used to determine carbon apparently provides lower estimates (an average here of 58% lower) than the high temperature combustion technique we used. Sharp (1973) found that persulfate oxidation yields an average 22% lower values than high temperature combustion when these methods are used to measure total organic carbon in seawater.

In terms of variability, the observations of Platt et al. (1969) have a variance from the regression line significantly ($P<0.01$) larger than ours by a factor of 1.6.

It is clear from the comparisons of biomass measures we have carried out, and from other unpublished work performed at this laboratory, that the techniques used by various investigators in determining a particular biomass measure (such as displacement volume) provide substantially different answers which are not readily comparable. This is particularly true of displacement volume and wet weight and to a lessor degree, carbon. A similar conclusion was reached by Nakai and Honjo (1962). Only the procedure for measuring dry weight described by Lovegrove (1966) seems to have been widely adopted and values presented by various investigators using this technique seem to be intercomparable. With displacement volume and wet weight, the problem stems largely from the differing amounts of interstitial water adhering to the zooplankton at the time of measurement. We have found, as did Nakai and Honjo (1962), that for a given technique, the amount of interstitial water varies inversely with the amount of biomass being measured. The amount, however, varies from technique to technique. Efforts to significantly reduce the amount of interstitial water present appear to create additional error. Rather than simply concentrating on the reduction of interstitial water, it is more important to establish a reproduceable procedure that generates values which can be directly related to a more absolute standard such as carbon as we have tried to do. The data on which Equations 1 to 6 and 11 to 13 in Table 2 are based were developed using methods which appeared to us to involve the least amount of technique-derived error and which required little complex instrumentation.

The zooplankton biomass values used in this study encompass a significant part of the range of values an investigator is likely to encounter working in either coastal waters or the open ocean. Thus, the equations we have presented should be useful in a wide variety of situations providing the same techniques to measure biomass are employed. It is important to bear in mind, however, that situations do occur in which these equations may not apply. One example is where marine populations are dominated by salps, doliolids, jellyfish, or chaetognaths. The very high percentage of intracellular water in these organisms may cause the relationships between displacement volume or wet weight and dry weight or carbon to deviate strongly from our predicted relationships. In such cases, which in our experience occur infrequently, we recommend that dry weight or carbon be measured directly.

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LITERATURE CITED

AHLSTROM, E. H., AND J. R. THRAILKILL.
1963. Plankton volume loss with time of preservation. Calif. Coop. Oceanic Fish. Invest. Rep. 9:57-73.

BÉ, A. W. H., J. M. FORNS, AND O. A. ROELS.
1971. Plankton abundance in the North Atlantic Ocean. *In* J. D. Costlow, Jr. (editor), Fertility of the sea 1:17-50. Gordon and Breach Sci. Publ., N.Y.

CURL, H., JR.
1962. Analyses of carbon in marine plankton organisms. J. Mar. Res. 20:181-188.

FROLANDER, H. F.
1957. A plankton volume indicator. J. Cons. 22:278-283.

LOVEGROVE, T.
1966. The determination of the dry weight of plankton and the effect of various factors on the values obtained. *In* H. Barnes (editor), Some contemporary studies in marine science, p. 429-467. George Allen and Unwin Ltd., Lond.

MCEWEN, G. F., M. W. JOHNSON, AND T. R. FOLSOM.
1954. A statistical analysis of the performance of the Folsom plankton sample splitter, based upon test observations. Arch. Meteorol. Geophys. Bioklimatol., Ser. A, 7:502-527.

MCGOWAN, J. A., AND D. M. BROWN.
1966. A new opening-closing paired zooplankton net. Univ. Calif., Scripps Inst. Oceanogr. Ref. 66-23, 56 p.

MENZEL, D. W., AND J. H. RYTHER.
1961. Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production. J. Cons. 26:250-258.

NAKAI, Z., AND K. HONJO.
1962. Comparative studies on measurements of the weight and the volume of plankton samples. A preliminary account. Indo-Pac. Fish. Counc. Proc., 9th Sess., Sect. II, p. 9-16.

PLATT, T., V. M. BRAWN, AND B. IRWIN.
1969. Caloric and carbon equivalents of zooplankton biomass. J. Fish. Res. Board Can. 26:2345-2349.

PLATT, T., AND B. IRWIN.
1968. Primary productivity measurements in St. Margaret's Bay. 1967. Fish. Res. Board Can., Tech. Rep. 77, 123 p.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

SHARP, J. H.
1973. Total organic carbon in seawater–comparison of measurements using persulfate oxidation and high temperature combustion. Mar. Chem. 1:211-229.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1965. A manual of seawater analysis. 2nd ed., revised. Bull. Fish. Res. Board Can. 125, 203 p.

SUTCLIFFE, W. H., JR.
1957. An improved method for the determination of preserved plankton volumes. Limnol. Oceanogr. 2:295-296.

TRANTER, D. J.
1960. A method for determining zooplankton volumes. J. Cons. 25:272-278.

VACCARO, R. F., G. D. GRICE, G. T. ROWE, AND P. H. WIEBE.
1972. Acid-iron waste disposal and the summer distribution of standing crops in the New York Bight. Water Res. 6:231-256.

WIEBE, P. H., G. D. GRICE, AND E. HOAGLAND.
1973. Acid-iron waste as a factor affecting the distribution and abundance of zooplankton in the New York Bight. II. Spatial variations in the field and implications for monitoring studies. Estuarine Coastal Mar. Sci. 1:51-64.

YENTSCH, C. S., AND J. F. HEBARD.
1957. A gauge for determining plankton volume by the mercury immersion method. J. Cons. 22:184-190.

EFFECTS OF VARIOUS CONCENTRATIONS OF DISSOLVED ATMOSPHERIC GAS ON JUVENILE CHINOOK SALMON AND STEELHEAD TROUT

EARL M. DAWLEY AND WESLEY J. EBEL[1]

ABSTRACT

Bioassays in shallow tanks (25 cm deep) with dissolved nitrogen and argon gas concentrations ranging from 100 to 125% of saturation in water at 15°C were conducted to determine lethal and sublethal effects on juvenile chinook salmon, *Oncorhynchus tshawytscha*, and steelhead trout, *Salmo gairdneri*. Significant mortality of both species commenced at 115% saturation of nitrogen and argon (111% saturation of total dissolved atmospheric gas pressure). Over 50% mortality of both steelhead and chinook occurred in less than 1.5 days in water at 120 and 125% of saturation. Significant differences in swimming performance, growth, and blood chemistry were measured in groups of fish tested at sublethal exposures in various concentrations of dissolved gases. Sublethal stress for 35 days at 110% dissolved nitrogen (106% total atmospheric gas) decreased normal swimming ability of chinook. Growth of both steelhead and chinook was affected by sublethal exposures in water saturated with atmospheric nitrogen and argon at 105, 110, and 115%. Blood chemistry was affected at sublethal exposures in water at 115% saturation.

Supersaturation of atmospheric gas (mainly nitrogen) in waters of the Columbia and Snake rivers—caused by spillway discharges from dams—has been well documented as a serious problem to valuable stocks of Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*. Gas bubble disease resulting from this supersaturation causes both direct and indirect mortalities. Direct mortality results from air emboli in the heart and gill filaments, destruction of vital organs, or characteristic red blood cell hemolysis (Marsh and Gorham 1905; Pauley and Nakatani 1967; Bouck et al. 1970[2]). Indirect mortality is a consequence of later invasion by disease organisms (Coutant and Genoway 1968[3]) or of increased predation due to reduced performance capabilities of the fish as the result of sublethal exposure to supersaturation.

The lowest level of nitrogen supersaturation at which juvenile salmon or steelhead trout can be exposed continually with no detrimental effects is not known. Several investigators have recorded the lowest level observed during various experiments where mortalities occurred from gas bubble disease; however, very little attention has been given to determining the effect of sublethal exposure on physiological and behavioral performance. Harvey and Cooper (1962) indicated 108-110% saturation produced gas bubble disease and subsequent mortalities in sockeye salmon alevins, *O. nerka*; Rucker and Tuttle (1948) indicated a level somewhere between 110 and 115% as being the critical range for trout. Shirahata (1966) conducted the most comprehensive study to date on the effects of various levels of nitrogen gas on rainbow trout (rainbow trout is the nonanadromous form of *S. gairdneri*, whereas the steelhead trout is the anadromous) from hatching to the swim-up stage, but such detail is lacking for other species of salmonids. In many experiments on gas bubble disease, either the water temperatures, nitrogen gas concentrations, or life stages of the test fish were omitted from record, thus making the results incomplete for critical applications.

Costs involved in alleviating the supersaturation problem in the Columbia and Snake rivers will be considerable. The extent of these costs will depend on the degree of protection required to afford a safe environment for the aquatic biota. It is imperative, therefore, that regulatory measures established to govern the level of saturation be

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[1] Northwest Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2] Bouck, G. R., G. A. Chapman, P. W. Schneider, Jr., and D. G. Stevens. 1970. Observations on gas bubble disease in adult Columbia River sockeye salmon (*Oncorhynchus nerka*). Pac. Northwest Water Lab. [Fed. Water Qual. Adm., Corvallis, Oreg.], June 30, 1970. Unpubl. manuscr. 19 p.

[3] Coutant, C. C., and R. G. Genoway. 1968. Final report on an exploratory study of interaction of increased temperature and nitrogen supersaturation on mortality of adult salmonids to U.S. Bur. of Commercial Fisheries, Seattle, Washington. Battelle Mem. Inst. Pac. Northwest Lab. Richland, Wash., November 28, 1968, 28 p.

Manuscript accepted February 1975.

based upon a thorough understanding of the effects of dissolved gases on aquatic organisms.

This paper describes the results of dissolved gas bioassays with juvenile steelhead trout and spring chinook salmon, *O. tshawytscha*, conducted by the National Marine Fisheries Service during the spring of 1972. These experiments were designed to assess lethal and sublethal effects of supersaturation of atmospheric gases on test fish at levels found in the Columbia and Snake rivers during the spring freshet. Atmospheric nitrogen concentrations[1] were of major concern and test levels ranged from 100 to 125% of saturation. Special note is made of testing procedures and ramifications of the effects of these on the outcome of our tests.

METHODS

Bioassays were carried out in the laboratory in shallow tanks (25-cm water depth) to negate the effects of hydrostatic pressure compensation. These facilities were similar to those described by Ebel et al. (1971). Water flow into each test tank was maintained at 3 liters/min at a temperature of 15° ± 0.5°C. Test tanks were partitioned with perforated fiberglass plates to form four sections —in-flow area, test area A, test area B, and outflow section (Figure 1).

Supersaturated water was produced by metering 0.7 liter/min air into the suction side of a centrifugal pump which recirculated water through a 197-liter (52-gallon) closed receiver at a rate of about 190 liters/min (50 gal/min). Water pressure throughout the system was at 1.4 kg/cm^2 (20 psi) except in a short section of pipe on the discharge side of the pump where it was increased to 3.2 kg/cm^2 (45 psi) by use of a valve for additional back pressure necessary to achieve the required supersaturation. Water remained in the recirculatory system for about 10 min before passing to the test tanks. This arrangement supersaturated the water to about 145% of air saturation. Water was then piped to the test tanks where it passed over a series of perforated fiberglass plates into an inlet box with air bubbling through a bottom plate of porous polyethylene. The number of fiberglass plates and volume of air were adjusted to yield the various levels of saturation. An increase of air to water interface directly decreased the excess dissolved gas content.

Water samples for dissolved gas analyses were collected throughout the tests near the center of each test tank directly in front of the partition between A and B testing areas and in some tests at the center of each section of the tank. Frequency of analysis varied from once an hour to once a day depending on duration of test. Procedure for analysis of dissolved nitrogen was from Van Slyke and Neill (1924) using manometric blood gas apparatus; dissolved oxygen was analyzed using modified Winkler procedures

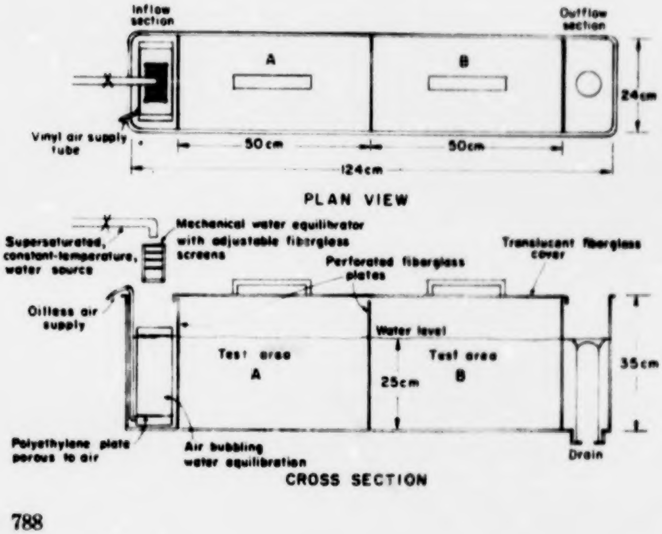
Inflow section
Outflow section
A
B
24cm
Vinyl air supply tube
50cm
50cm
124cm
PLAN VIEW
Mechanical water equilibrator with adjustable fiberglass screens
Supersaturated, constant-temperature, water source
Translucent fiberglass cover
Perforated fiberglass plates
Oilless air supply
Water level
Test area A
Test area B
25cm
35cm
Polyethylene plate porous to air
Air bubbling water equilibration
Drain
CROSS SECTION

FIGURE 1.—Plan and cross-sectional views of test tank used for bioassay of dissolved gas.

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[1] Atmospheric nitrogen—nitrogen gas (98.8% by vol) plus argon gas (1.2% by vol) hereafter referred to as nitrogen or N_2 + Ar.

(American Public Health Association et al. 1971). Gas concentrations at saturation (100%) were taken from Weiss (1970).

To obtain the dissolved gas levels for the various tests, we adjusted the water equilibrators of each tank (screens plus air bubbling boxes) until the nitrogen concentration remained within ±2% of the desired value. The oxygen concentration was then measured and we found that the saturation value was 5 to 10% lower than that of N_2+ Ar for each tank. This did not differ appreciably from prevailing oxygen saturations in the Columbia and Snake rivers which are usually 5 to 10% lower than dissolved nitrogen values (Beiningen and Ebel 1971; Ebel 1971). After introducing fish, however, we noted that the oxygen concentration dropped further (presumably because it was consumed), resulting in values from 8 to 28% of saturation below that of N_2 + Ar, particularly in test area B and the outlet area of the tank. Due to large numbers of fish required for experiments on the survivors of these bioassays, and the complexity of changing the dissolved gas ratios of the water source, we did not alter the O_2 concentrations in the tests but carefully documented the mid-tank gas concentrations. Data affected by this drop in oxygen partial pressure are discussed later in this report.

One-year-old spring chinook salmon from Leavenworth National Fish Hatchery, Leavenworth, Wash., and steelhead trout from the Washington Department of Game Hatchery at Aberdeen, Wash., were used in the tests. Test populations were acclimated to laboratory water at 15°C with normal dissolved gas concentrations for at least 2 wk before testing. Groups of 30 or 60 fish were placed simultaneously in control (100% atmospheric nitrogen saturation) and test tanks set at 105, 110, 115, 120, and 125% of N_2 + Ar saturation and one to four replicates of each test were made, depending on test level. When 60 fish were being tested, 30 were in each of the two test sections A and B. Fish were randomized before introduction into individual test tanks. Mean sizes of the fish at completion of the tests are indicated in Table 1. Measurement of size at the beginning of the tests was omitted to avoid placing additional stress on the test animals. Feeding of fish during the test period began 48 h after introduction to test tanks; thereafter they were fed to satiation once each weekday.

Lethal exposure times to 10 and 50% mortality (LE_{10} and LE_{50}) were averaged for lots of test fish held in tank sections A and B during the same time period, and the mid-tank gas concentrations were used for analysis with the exception of the steelhead groups stressed at 115% nitrogen; in these tests, exposure times and gas concentrations were measured separately for A and B sections of the tanks. In addition, lethal exposure times to 100% mortality (LE_{100}) for chinook and steelhead at all levels of supersaturation were taken only from groups held in the A section of the tanks.

Observations of behavior, progression of external signs of gas bubble disease, and mortality were recorded continuously for the first 6 h then every ½ h for 24 h and every 3, 6, or 12 h thereafter – depending on test concentration – until termination of the bioassay at 35 days. Observations of change in degree of external disease signs among test fish after a recovery period in normally saturated (100%) water also were made from selected groups.

Sublethal effects of supersaturation were as-

TABLE 1.–Comparison of mean weights and lengths of surviving test and control fish held in 15°C water with N_2 + Ar levels at 100 to 125% of saturation, February-April 1972.

Test level (% of saturation of N_2 + Ar)	Testing period[1] (mo/day)	Duration (individual tests)	Test fish		Control fish (100% N_2 + Ar)	
			Weight (g)	Length (mm)	Weight (g)	Length (mm)
			Spring chinook salmon			
105	2/8-3/14	35 days	13.6	115	15.5	119
110	3/7-4/11	35 days	17.5	125	17.9	126
115	2/8-3/14	35 days	13.6	115	15.5	119
120	2/8-3/3	≤55 h	16.2	120	18.0	122
125	2/8-3/1	≤38 h	16.8	117	16.8	118
			Steelhead trout			
105	4/3-5/8	35 days	18.8	130	22.8	135
110	4/10-5/15	35 days	20.0	130	22.0	132
115	4/13-5/13	≤35 days	19.8	130	20.9	132
120	4/3-4/18	≤53 h	20.6	124	—	—

[1] Replicates of tests at 115-125% levels were made at various time intervals throughout the indicated test period; others lasted the full indicated period.

sessed by using measurements of maximal swimming performance, blood chemistry, and photic response. Measurements were made on groups of survivors from lethal exposure tests immediately after the LE_{10} and LE_{50} points were reached or following a 2-wk recovery period in 100% saturated water. Swimming performance was measured by distance gained and time of swimming against a constant water current of 1.25 m/s within a U-shaped inclined trough (14 m long and 8 cm wide). Blood samples were analyzed on a Technicon Sequential Multiple Analyzer (SMA 12/60).[5] Pooled serum samples were analyzed for Ca, Na, PO_4, K, Cl, albumin, total protein, cholesterol, alkaline phosphatase, glucose, urea, uric acid, total bilirubin, lactic dehydrogenase and serum glutamic oxaloacetic-acid transaminase. Photic response was evaluated by electrophysiological monitoring of the optic tectum during retina stimulation with flickering light. A more detailed description of the methods used in the swimming performance and blood chemistry measurements appear in reports by Schiewe (1974) and by Newcomb (1974),[6] respectively.

RESULTS

Relationships Among Mortality, Exposure Time, and Gas Concentration

Mean exposure times at which 10, 50, and 100% mortality occurred at 120 and 125% N_2 + Ar saturation indicate no substantial difference between susceptibility of juvenile chinook and steelhead trout (Table 2). However, at 115% N_2 + Ar saturation, steelhead appeared to be more susceptible than chinook; i.e., steelhead reached the 50% mortality level within 35 days, whereas LE_{50} was never reached in test groups of chinook.

Mortalities of control fish for all tests (105-125%) ranged from 0 to 3.3% throughout the 35-day test periods. Because of the comparatively minor losses of controls, data from test groups are given as observed (not compensated for loss of controls). Mortalities observed in tests at 105 and 110% of nitrogen saturation were 5% or less for both species, and gas bubble disease was not the apparent cause of death.

The onset of mortality attributable to gas supersaturation occurred at about 115% dissolved nitrogen among both steelhead and chinook.

At about 120% nitrogen saturation the means of lethal exposure times to 50% mortality (LE_{50}) were 26.9 and 33.3 h for chinook and steelhead, respectively. LE_{50}'s for chinook and steelhead at 125% nitrogen saturation were 13.6 and 14.2 h, respectively, which are similar to those (11.3 and 14.0 h) observed in earlier tests by Ebel et al. (1971) at test concentrations of 125 to 130% N_2+ Ar. Test fish stocks used previously were from different hatcheries and earlier brood years and were slightly larger (spring chinook–23 g and 135 mm, steelhead–54 g and 179 mm).

TABLE 2.–Mean values of lethal exposure time for juvenile steelhead and chinook acclimated to 15°C and then subjected to various levels of gas saturation[1] from 100 to 125% in shallow tanks (25-cm depth).

Percent saturation (N_2 + Ar)	Percent mortality	Exposure time (h)	
		Steelhead	Chinook
125	10	10.3	10.6
	50	14.2	13.6
	100	[2]23.0	[2]32.1
120	10	26.0	10.3
	50	33.3	26.9
	100	[2]40.0	[2]55.0
115	10	[2]258.0	(7% mortality in 792 h)
	50	[2]486.0	Not reached
	100	Not reached	Not reached
110 105 100	Mortality of 5% or less recorded for either steelhead or chinook after 35 days at these concentrations. Gas bubble disease was not apparent cause of deaths.		

[1] Percentage saturation of nitrogen and argon was set as indicated in the table (± 2%). Oxygen concentrations ranged between 87 and 96% saturation in tanks set at 100-110% nitrogen plus argon saturation; in tanks set a 115-125% nitrogen saturation, O_2 levels ranged between 98 and 115%.

[2] Exposure times indicated for test replicates of section A only. Mortality in section B had not reached indicated level at termination of test.

Effect of Oxygen Concentrations on Time to Death Measurements

The role of atmospheric gases other than nitrogen (particularly oxygen) in causing gas bubble disease has been questioned by several investigators. Arguments for and against the assumption that dissolved atmospheric nitrogen is the exclusive cause of gas bubble disease are prevalent throughout the literature (Marsh and Gorham 1905; Doudoroff 1957; Egusa 1959, 1969; Shirahata

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[5] Trade names referred to in this publication do not imply endorsement of commercial products by the National Marine Fisheries Service, NOAA.

[6] Newcomb, T. W. 1974. Changes in juvenile steelhead (*Salmo gairdneri*) blood chemistry following sublethal exposure to various levels of nitrogen supersaturation. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash. Unpubl. manuscr.

1966; Bouck 1972[1]; Rucker 1972). Most of the comprehensive studies, however, have been analyzed in terms of nitrogen concentration, assuming it to be the controlling influence upon the effects of gas bubble disease (even greater than indicated by the 80/20 ratio of the partial pressures N_2/O_2). This assumption was based upon supposed biochemical decrease of the effective oxygen partial pressure within the fish.

In comparing data from this experiment with that from past research we should acknowledge that our primary criterion during planning and set-up stages was dissolved nitrogen + argon concentration. At the outset of these experiments, oxygen levels were monitored primarily for documentation of overall water quality rather than for use in analysis of their effect upon the test organisms. However, upon examination of initial results derived from each of the tests carried out to lethal exposures, we found that the times for LE_{10} and LE_{50} were consistently less in test section A than in Section B. Analyses of individual gas pressures in each of the two sections of the tanks were made to determine whether variations occurred among the component gases. We found that nitrogen concentrations were constant in both areas, but oxygen concentrations remained consistently lower (5-10%) in section B than in section A. The lower oxygen concentrations–thus lower (1-2%) total dissolved gas (TDG) saturations–appeared directly correlated with the lower mortality rates in section B of the test tanks. For example, when we examined mortality rates of individual groups of steelhead from A and B test sections at 115% N_2 + Ar, we found: N_2 + Ar saturation (in section B) of 116.0% and 88.2% of O_2 saturation (TDG at 110.0% of saturation) caused no mortality in 35 days for one replicate of 30 fish, whereas N_2 + Ar saturation (in section A) of 116.0% and 98.8% O_2 (TDG at 112.1%) caused 50% mortality in an average of 20 days for two replicates.

Effect of Supersaturation Stress on Growth

Exposure to sublethal concentrations (concentrations at which no substantial mortality occurred within 35 days) of N_2+Ar appeared to affect growth of both juvenile chinook and steelhead. Mean weights and lengths of test fishes after 35 days in dissolved nitrogen concentrations of 105, 110, and 115% of saturation (Figure 2) were in each instance less than those of controls.

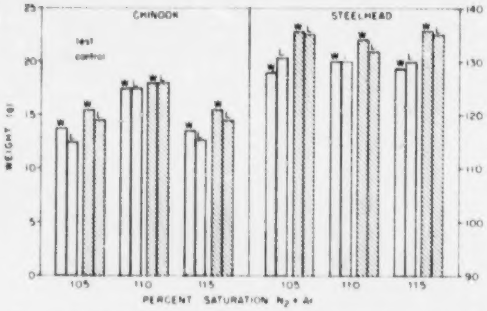

FIGURE 2.–Comparison of mean weights (W) and lengths (L) for test and control groups of juvenile chinook salmon and steelhead trout after 35 days at saturation levels of 100% (control), 105%, 110%, and 115%.

A statistical test of the hypothesis–that the slopes of the regression of mean weight of control fish groups and mean weight of test fish groups were equal–yielded a value of t = 4.938 (P<0.02 at 4 df). The same statistical test of mean lengths of control vs. test groups yielded t = 1.36 (P<0.25 at 4 df). The lower t value calculated from length data is attributable to the duration of the test not being long enough to significantly overcome the variation in lengths between individuals within groups. We attribute the difference between size of test and control lots to the effect of supersaturation on the normal growth of the test fish.

After 30 days of testing at the 115% level, feeding response of the chinook fingerlings became lethargic. Many of the test fish had spinal flexures, exophthalmia, and large buccal cavity gas blisters and were unable or unwilling to move and accept food when made available. By contrast, control fish exhibited aggressive feeding behavior throughout the tests. Gross gas bubble disease signs and behavioral changes were less evident at 110% N_2 + Ar and nonexistant at 105%.

Testing for changes in the condition factor of juvenile fall chinook and steelhead during long-term (2-4 mo) holding in water saturated 100 to 127% N_2+Ar is currently underway. Results of these tests may provide further information on effects of gas supersaturation on growth rate.

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[1] Bouck, G. R. 1972. Effects of gas supersaturation on salmon in the Columbia River. West. Fish. Toxicol. Stn., Environ. Prot. Agency, Corvallis, Oreg. Paper presented at Ecol. Soc. Am. Symp. Aug. 1972, 29 p.

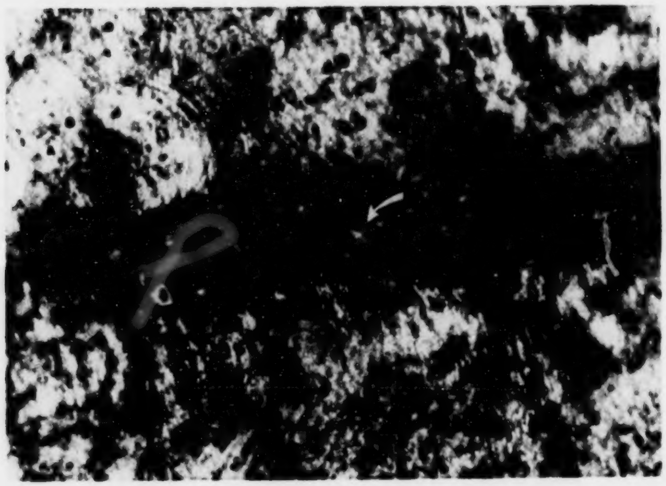

FIGURE 3.–Gas bubbles (arrow) in lateral line of juvenile chinook salmon.

Progression of Gas Bubble Disease

Observations on the progression of external signs of gas bubble disease in spring chinook exposed to various levels of supersaturation revealed that the first developments such as bubble formation in the lateral line (Figure 3) appear within 2 h of exposure at 125%. Subcutaneous gas blisters between fin rays of at least one fin were present on each of the test animals before 11.5 h at 125%, and before 55 h at the 120% level. Several days' exposure were required before these signs occurred on fish tested at 115%. After 35 days, 56% of the fish at 110% had lateral line bubbles but only 4% had fin bubbles. Exophthalmia or "popeye," hyphema, cutaneous blisters of the head and buccal cavity, and spinal flexures were absent among fish tested at 120 and 125% but began appearing after 6 days on fish held at 115% and after 11 days on those held at 110% of nitrogen saturation. Apparently at the higher saturation levels, the fish died from cardiac occlusion or branchial artery occlusion (Figure 4) before development of these signs. By the end of 35 days, fish held at 115%

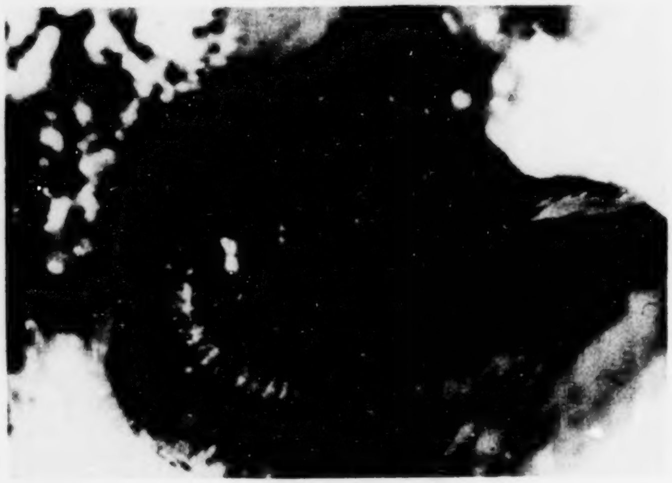

FIGURE 4.–Gas emboli occluding gill filaments and branchial artery of chinook salmon held in 125% nitrogen saturation for 20 h.

exhibited more than a 75% incidence of exophthalmia, 20% of the fish had spinal flexures, and 25% of the fish in section A became more or less immobile. After 35 days of exposure at 110% N_2 + Ar, only 12% of the test fish exhibited signs other than the lateral line bubbles. No apparent signs of gas bubble disease were observed in fish tested at 105% nitrogen.

Development of gas bubble disease signs in steelhead was similar to that of chinook–the signs occurred in the same sequence but the exposure time required to produce the signs was slightly less.

Recovery From Gas Bubble Disease

Observations on disappearance of gas bubble disease signs and delayed mortality following tests were made on groups of survivors of fish stressed to the LE_{50} level at 120, 125, and 130% of saturation. These survivors were placed in water at 100% gas saturation for up to 15 days. No delayed mortality could be attributed to prior exposure to supersaturation in either the chinook or the steelhead. The only significant mortality in any recovery group was a 10% loss of one replicate of steelhead subjected to 125% N_2+ Ar until LE_{50}, followed by a burst swimming performance test. Some mortality occurred after 102 h of recovery time, but the only observable disease sign was the presence of lateral line bubbles on one fish. Other mortalities during recovery were less than 3% of the fish held; no gas bubble disease signs were found. All external symptoms that were readily visible at the time the fish were removed from the recovery tanks had disappeared after 15 days in both species.

Steelhead that had undergone 16, 24, and 35 days' exposure at 115% nitrogen saturation still showed gas bubbles after being held 3 days in normally (100%) saturated water. After 1.5 days' recovery, 64% exhibited lateral line bubbles or fin ray gas blisters and one fish (7%) retained unilateral exophthalmia; after 2 days' recovery, 88% of another group retained signs of lateral line bubbles and fin gas blisters; at 3 days, 54% of the third group retained like signs of gas bubble disease. After 15 days' recovery, no gas bubble disease signs were observed on groups of test fish examined.

Effect of Supersaturation Stress on Survivors

Burst swimming performance and blood chemistry were examined as potential indices of stress from sublethal exposures to supersaturated water.

Swimming performance (Schiewe 1974) of chinook that survived from tests at 110-125% was significantly lower than that of control fish. Visual observations of behavior during swimming performance tests indicated genuine debilitation (inability to swim in some cases) which in turn resulted in lower swimming performance (i.e. less distance gained and less swimming time against a constant water current stimulus). No difference was apparent between performance of chinook salmon tested at 105% saturation and the control fish.

Swimming performance of steelhead trout that survived tests at 105-125% was not significantly different from the performance of control fish. Performance of test and control lots of steelhead trout was highly variable. Fish stressed by exposure to supersaturation often responded in an irritated or stimulated fashion, which often resulted in a high measure of performance. Further tests with steelhead are needed to determine whether swimming performance is a useful index of stress from supersaturation and, if so, whether test results in the laboratory apply to survival of fish in the river.

Blood serum from groups of chinook and steelhead surviving supersaturation tests to LE_{10} and LE_{50} were analyzed (Newcomb see footnote 6) using a SMA 12/60. A 5% decrease in serum calcium was noted in chinook exposed to 115% nitrogen plus argon when compared to those exposed to lower levels of supersaturation. Steelhead exposed to 115% nitrogen showed a 10 to 17% decrease in serum calcium and a decrease in serum albumin, total protein, serum chloride, cholesterol, and in alkaline phosphatase activity when compared to controls and those exposed to lower saturations. No significant changes in blood serum components were observed in samples taken from test groups exposed to levels of 105 and 110% of saturation when these were compared with controls.

Measurements of photic response of salmonids failed to provide any consistent evidence of stress-related phenomena due to supersaturation so these tests were discontinued.

DISCUSSION

Data from these tests indicate that the critical level of supersaturation of nitrogen where juvenile spring chinook and steelhead began to show mortality was about 115% N_2+Ar when O_2 saturations were about 95% (111% TDG). These data agree closely with the findings of Shirahata (1966), who indicated that the critical level for 2-mo-old rainbow trout was about 111.3%, N_2+Ar and 99.7% O_2 (109% TDG).

Although mortality from supersaturation did not occur until fish were exposed beyond 110% (± 2%) N_2 + Ar, swimming performance measurements with juvenile chinook showed some effect from stress caused by exposure to supersaturation at levels as low as 110% N_2 + Ar (106% TDG). We believe that one can infer from the results of these tests, that something less than normal survival will result when juvenile chinook and steelhead are exposed for 35 days or longer at or above 110% N_2+Ar (106% TDG).

Results of our testing program indicate that oxygen as well as nitrogen is responsible for causing gas bubble disease, even when O_2 concentrations are below saturation. The immediate conclusion drawn from this observation would be that total dissolved gas is the cause rather than any one or combination of component atmospheric gases. However, fish tolerance research by Egusa (1969) and by Rucker (1975) with various ratios of dissolved gas indicate that mortality from gas bubble disease is not necessarily in linear correlation with TDG. Egusa showed that oxygen saturation values of 400 to 500% were required to produce initial mortality of goldfish, *Carassius auratus*, and an eel *Anguilla japonica* when nitrogen concentrations were near 100% (TDG 160-180%). In earlier work with the same two species, however, Egusa (1959) recorded high mortality of goldfish with N_2+Ar at 132% and O_2 at 75% of saturation (TDG 123%), and of eel with N_2+Ar at 124%, O_2 at 66% (TDG 112). Rucker found that mortality rate of juvenile salmon declines considerably if the ratio of oxygen to nitrogen is increased even though the same TDG pressure is maintained.

It is apparent from our tests and those of Egusa and Rucker that the ratio of O_2 and N_2 must be considered as well as TDG when assessing possible effects from supersaturation.

Additional information is needed to quantify the effects of various gas ratios (nitrogen to oxygen) on tolerance limits of fish in general. It is probable that most fish could tolerate higher total gas pressure if the major portion of the excess gas were oxygen.

Dissolved gas measurements and resulting percentage saturations for the Columbia and Snake rivers (Ebel 1969, 1971; Beiningen and Ebel 1971) have been based on surface or atmospheric pressure plus vapor pressure. Corrections for the hydrostatic pressure (or depth) at which a sample was taken were not made. Thus, the calculations of percentage saturation were made as though the samples were collected at the surface. This is convenient when limnologists or oceanographers wish to compare values taken at various depths, but leads to confusion when attempting to assess how a given saturation measurement will affect a fish at depth.

The depth that populations of fish travel must be considered when one attempts to determine the effects of an exposure to supersaturated levels of dissolved gases. Bubble formation in the circulatory system or tissues of fish is directly dependent on the external hydrostatic pressure. For example, a fish traveling at a depth of only 1 m will be provided with enough hydrostatic pressure to compensate for a gas pressure in excess of 10% (110% saturation at surface pressures). A fish traveling at 3 m can compensate for 30%, or 130% saturation at surface pressures; a fish traveling at 10 m can compensate for an excess of 100% of saturation and so on. These tests were conducted in shallow tanks at essentially zero hydrostatic pressure with only a few centimeters depth compensation possible. The lethal exposure times we measured could only be applied directly to fish populations that could not compensate by sounding. Much more information is needed to determine how a given gas level in a river affects the population inhabiting the river. Information regarding the behavior of fish is obviously essential. We believe, however, that data from our tests support the 110% maximum allowable limit established by the Environmental Protection Agency primarily because significant mortalities did not occur until concentrations exceeded 110% TDG.

Gas bubble disease signs either singly or in combination with one another did not correlate well with mortality. Those generated from stress conditions of 120% saturation and higher seemed to be nearly the same at LE_{10} as at LE_{100} (gas blisters in the fins and lateral lines of most live and dead fishes). Signs that developed at lower levels (110-115%) were obviously different from those appearing at the higher saturations; i.e., gas blisters in and around the eye, exophthalmia, cutaneous gas blisters on the head and in the mouth, and spinal flexures. Neither set of signs (low-level or high-level types) correlate by percent of incidence or severity, with accumulative mortality. But they showed that one could determine with reasonable accuracy, whether fish observed in the river had been exposed to supersaturation for a long or short duration. Populations with signs of chronic exposure (exophthalmia, spinal flexures, etc.) could have been either 1.5 to 2.0 m deep in highly supersaturated water (130-135%) or near the water surface at near 115% saturation.

SUMMARY AND CONCLUSIONS

Bioassays in shallow tanks (25 cm) with dissolved nitrogen and argon gas concentrations ranging from 100 to 125% of saturation were conducted to determine lethal and sublethal effects on juvenile chinook salmon and steelhead trout.

Juvenile steelhead (130 mm fork length) reached the LE_{50} level within 35 days when exposed to 115% of nitrogen and argon saturation (112% TDG), whereas mortality of juvenile chinook (115 mm) did not exceed 7%. There appeared to be no substantial difference between susceptibility of chinook and steelhead at 120 or 125% saturation N_2 + Ar. No mortality related to supersaturation occurred in either juvenile chinook or steelhead trout exposed to 110 or 105% saturation N_2 + Ar. Signs of gas bubble disease (such as bubbles in lateral line and exophthalmia) were evident on both species, however, after 35 days exposure to 110%.

Time to death decreased in test tanks with higher oxygen concentrations (thus higher TDG) even though nitrogen and argon concentrations were identical, indicating that oxygen as well as nitrogen and argon concentrations must be considered when time to death values are compared.

The first notable sign of gas bubble disease was appearance of bubbles in the lateral line which appeared in some degree at all gas concentrations tested. Exophthalmia, dermal gas blisters of the buccal cavity and cephalic regions, and spinal flexures did not occur with short-term exposure (6 days) or at the higher levels (120 and 125%) but was prevalent after long exposure at both 115 and 110% saturation N_2 + Ar. External gas bubble disease signs disappeared within 15 days when fish were placed in normally saturated water (100%).

Fish stressed with supersaturation at sublethal levels for 35 days grew less than controls and the swimming performance of juvenile chinook exposed for sublethal periods to 110-125% nitrogen saturation was significantly lower than controls. Blood chemistry measurements indicated that significant differences occurred between blood samples taken from test and control chinook and steelhead after they were exposed to levels of 115% saturation. Serum calcium, for example, was 10-17% lower in samples taken from test groups of steelhead.

We concluded from these experiments that:

1. Significant mortality of both juvenile chinook and steelhead trout commences at about 115% saturation of nitrogen and argon (111% TDG).
2. Sublethal exposures to various concentrations of dissolved gas significantly affects swimming performance, growth and blood chemistry of chinook, and growth and blood chemistry of steelhead trout.
3. The first externally evident sign of gas bubble disease on juvenile chinook and steelhead trout exposed to supersaturation occurs as bubbles in pores of the lateral line.
4. Fish returned to normally (100%) saturated water appear to recover within 15 days from exposure to supersaturated water.

LITERATURE CITED

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION.
1971. Standard methods for the examination of water and wastewater. 13th edition. Am. Public Health Assoc., Wash., D.C., 874 p.

BEININGEN, K. T., AND W. J. EBEL.
1971. Dissolved nitrogen, dissolved oxygen, and related water temperatures in the Columbia and lower Snake rivers, 1965-69. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Data Rep. 56, 60 p. on 2 microfiche.

DOUDOROFF, R.
1956. Water quality requirements of fishes and effects of toxic substances. *In* M. E. Brown (editor), The physiology of fishes 2:403-430. Academic Press Inc., N.Y.

EBEL, W. J.
1969. Supersaturation of nitrogen in the Columbia River and its effect on salmon and steelhead trout. U.S. Fish Wildl. Serv., Fish. Bull. 68:1-11.
1971. Dissolved nitrogen concentrations in the Columbia and Snake Rivers in 1970 and their effect on chinook salmon and steelhead trout. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-646, 7 p.

EBEL, W. J., E. M. DAWLEY, AND B. H. MONK.
1971. Thermal tolerance of juvenile Pacific salmon and

steelhead trout in relation to supersaturation of nitrogen gas. Fish Bull., U.S. 69:833-843.

EGUSA, S.

1959. The gas disease of fish due to excess of nitrogen. [In Jap., Engl. summ.] J. Fac. Fish. Anim. Husb., Hiroshima Univ. 2:157-182.

1969. Yozon sanso kajo ni yoru sakana no gasu-byo ni tsuite (Gas disease of fish due to excess dissolved oxygen). Fish Pathol. 4:59-69. (Partial transl., Bur. Sport Fish Wildl., West. Fish. Dis. Lab., Seattle, Wash.)

HARVEY, H. H., AND A. C. COOPER.

1962. Origin and treatment of a supersaturated river water. Int. Pac. Salmon Fish. Comm., Prog. Rep. 9, 19 p.

MARSH, M. C., AND F. P. GORHAM.

1905. The gas disease in fishes. [U.S.] Bur. Fish., Rep. U.S. Comm. Fish. 1904:343-376.

PAULEY, G. B., AND R. E. NAKATANI.

1967. Histopathology of "gas-bubble" disease in salmon fingerlings. J. Fish. Res. Board Can. 24:867-871.

RUCKER, R. R.

1972. Gas-bubble disease of salmonids: a critical review. U.S. Fish Wildl. Serv., Bur. Sport Fish Wildl., Tech. Pap. 58, 11 p.

1975. Gas-bubble disease: Mortalities of coho salmon, *Oncorhynchus kitsutch*, in water with constant total gas pressure and different oxygen-nitrogen ratios. Fish. Bull., U.S. 73:915-918.

RUCKER, R. R., AND E. M. TUTTLE.

1948. Removal of excess nitrogen in a hatchery water supply. Prog. Fish-Cult. 10:88-90.

SCHIEWE, M. H.

1974. Influence of dissolved atmospheric gas on swimming performance of juvenile chinook salmon. Trans. Am. Fish. Soc. 103:717-721.

SHIRAHATA, S.

1966. Experiments on nitrogen gas disease with rainbow trout fry. [In Jap., Engl. abstr.] Bull. Freshwater Fish Res. Lab. 15(2):197-211.

VAN SLYKE, D. D., AND J. M. NEILL.

1924. The determination of gases in blood and other solutions by vacuum extraction and manometric measurement. I. J. Biol. Chem. 61:523-573.

WEISS, R. F.

1970. The solubility of nitrogen, oxygen, and argon in water and seawater. Deep-Sea Res. Oceanogr. Abstr. 17:721-735.

BIOLOGY AND TAXONOMY OF THE GENUS *NEMATOSCELIS* (CRUSTACEA, EUPHAUSIACEA)

K. GOPALAKRISHNAN[1]

ABSTRACT

The seven species of *Nematoscelis*, *N. difficilis*, *N. megalops*, *N. gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, and *N. lobata*, are described in a comparative manner, and keys for their identifications are provided. The key to the larvae is based on structural differences in the carapace and rostrum of furcilia stages, whereas the key to adults is mostly based on diagnostic features of the first thoracic leg (maxilliped) and a male secondary sexual structure, the petasma. *Nematoscelis gracilis* is represented by two distinct forms; they are considered ecophenotypes, since their patterns of geographical distribution appear correlated with differences in environmental characteristics, particularly the distribution of dissolved oxygen in the water column. Diagnostic features of these forms are pointed out. The antennule and carapace are sexually dimorphic in adults of all *Nematoscelis*. Abdominal photophores in the males show species-specific patterns of enlargement.

The genus *Nematoscelis* consists of seven species. It was described by G. O. Sars (1883, 1885) as consisting of *N. megalops*, *N. tenella*, *N. microps*, and *N. rostrata*. Hansen synonymized *N. rostrata* with *N. microps* and added four species: *N. gracilis* and *N. atlantica* in 1910, *N. difficilis* in 1911, and *N. lobata* in 1916. *Nematoscelis lobata* was not found by subsequent workers but the other species were discussed by Ruud (1936), Boden (1954), Boden et al. (1955) and Mauchline and Fisher (1969). Taxonomically *Nematoscelis* has been a difficult genus.

Like other species of euphausiids, *Nematoscelis* species have been identified mainly on the basis of differences in the male copulatory organ, the petasma. Since the petasma is an adult character, it has been difficult to identify immature specimens and mature females. Characters such as the shape of the eyes and structure of the second thoracic leg have been used to discriminate species. Einarsson (1942) showed structural differences in spermathecae (thelyca) of females, but such differences appear slight and are difficult to examine. Mauchline and Fisher (1969) pointed out difficulties encountered in the identification of species of this genus. In the present study an attempt is made to point out the diagnostic value of the first thoracic leg (maxilliped) in discriminating all species of *Nematoscelis*. This appendage usually remains attached to the animal caught by nets (as compared with the elongate second leg which is usually lost). It can be used as a diagnostic character in both sexes. The structural differences among the petasmae are also reexamined. The morphology of individual species will not be given separately, but species differences will be pointed out in a comparative manner. Since all species of this genus are sexually dimorphic, it is necessary to describe both sexes.

Another aspect to which little attention has been paid is the significance of developmental features in determining phylogenetic associations. Larvae of *Nematoscelis* are often difficult to separate as to species. The taxonomy of the larvae is yet to be worked out because the recognized adult characteristics are of no use in the larval identification. Gopalakrishnan (1973) summarized the available information on the sequential morphological development of an individual species. As Gordon (1955) and others have pointed out, larval characteristics may be more useful than those of adults in recognizing phylogenetic interrelationships of species. Adults show a greater degree of differentiation than the larvae, and their characters are more useful in the identification of the species than determining phylogeny. Moreover, part of the morphological variability observed in adults is sometimes ascribed to nongenetic modification that probably has no phylogenetic significance. Usually phylogenetic interrelationships are summarized in a classification. In this connection, larval characters are used

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extensively in classifying insect groups, such as Diptera and Hymenoptera. It is the intention of this taxonomic study to provide as much information as possible so that one can examine the systematic value of both larval and adult characters of *Nematoscelis*.

MATERIAL AND METHODS

The material used in this study consisted of 286 Isaacs-Kidd Mid-water Trawl (10 feet) collections and 1,950 plankton samples, including those collected during the International Indian Ocean Expedition (1960-65). These materials came from different geographical regions of the Atlantic, Indian, and Pacific oceans, mostly between lat. 40°N and 40°S. They are deposited at the Scripps Institution of Oceanography, La Jolla, Calif. All the trawl collections were not quantitative for estimating species abundance. A paper on the distribution and abundance of *Nematoscelis* based on plankton samples was already published (Gopalakrishnan 1974). Measurements were taken on 55 adult morphological characters for examining relative degree of differences. Ten males and ten females of each species were selected for these measurements. Statistical significance was determined on the basis of nonoverlapping confidence levels (95%) of the means. For making drawings, 10-20 individuals of each species were treated in heated 10% aqueous KOH to remove nonchitinous tissues. They were then stained in 1% aqueous Chlorazol Black E. Materials treated in KOH solution could be kept in 60-80% glycerol without shrinkage. Drawings were made with the aid of a camera lucida fitted to monocular and binocular microscopes.

The larval key was prepared on the basis of furcilia characters only. However, a few comments are made on characters of calyptopis and juvenile stages thought to have some diagnostic value. The adult key was prepared based on features of the first thoracic leg (maxilliped), eyes, antenna, and the carapace. Diagnostic features of the petasma are also included in the present key. Many characters are, therefore, used in the present key to facilitate its use on juveniles and adults of both sexes. Most of the commonly used adult characters are illustrated in Figure 1a. The terminology used here is the same that has been followed by most other workers. Larval terminology is defined and described in Gopalakrishnan (1973).

RESULTS

Larval Development

Between hatching and sexual maturity all species of *Nematoscelis* pass through four developmental phases: metanauplius, calyptopis, furcilia, and juvenile. A modified version of the nomenclature of larval development of euphausiids is given in Gopalakrishnan (1973). The metanauplius phase consists of one developmental stage, calyptopis of three (C_1, C_2, and C_3) and furcilia of three (F_1, F_2, and F_3). The strong differentiation of mouth parts and other thoracic legs shows similarities among larvae of all species of this genus. The development of larvae follows either of two pathways: *N. difficilis* and *N. megalops* follow one pathway and the other five species follow the other. During the third furcilia stage the second thoracic leg develops spines on both dactylus and propodus in *N. difficilis* and *N. megalops*, whereas in the rest of the species spines develop only on the dactylus. In all species of *Nematoscelis* this leg becomes the longest of all thoracic appendages.

Other developmental differences between the two species groups are as follows: during the juvenile phase, the maxillules of *N. difficilis* and *N. megalops* develop pseudexopods from the posterior face of the coxa as the four-setose larval exopods disappear; but in the remaining species, at about the same stage, the larval exopod disappears without the development of a pseudexopod. The lacina externa (lobes of basis) of the maxilla is trilobed in larvae of all species, but becomes bilobed in adults of *N. difficilis* and *N. megalops* and single lobed in adults of the remaining species.

The differences in the sequential development of pleopods and telson spines (terminal) are summarized in Figure 2. These features are consistent and appear to be characteristic of each subgroup. The terminal spines of the telson in species of both subgroups show differences not only in their sequential reduction but also in their external morphology (Figure 3A). This structural difference can be seen even during calyptopis stages of all species of this genus. This is a diagnostic feature and may have significance in understanding the evolution of the larvae. The dorsal keel and rostrum of the carapace also appear to be of important diagnostic value for furcilia (Figure 3B)

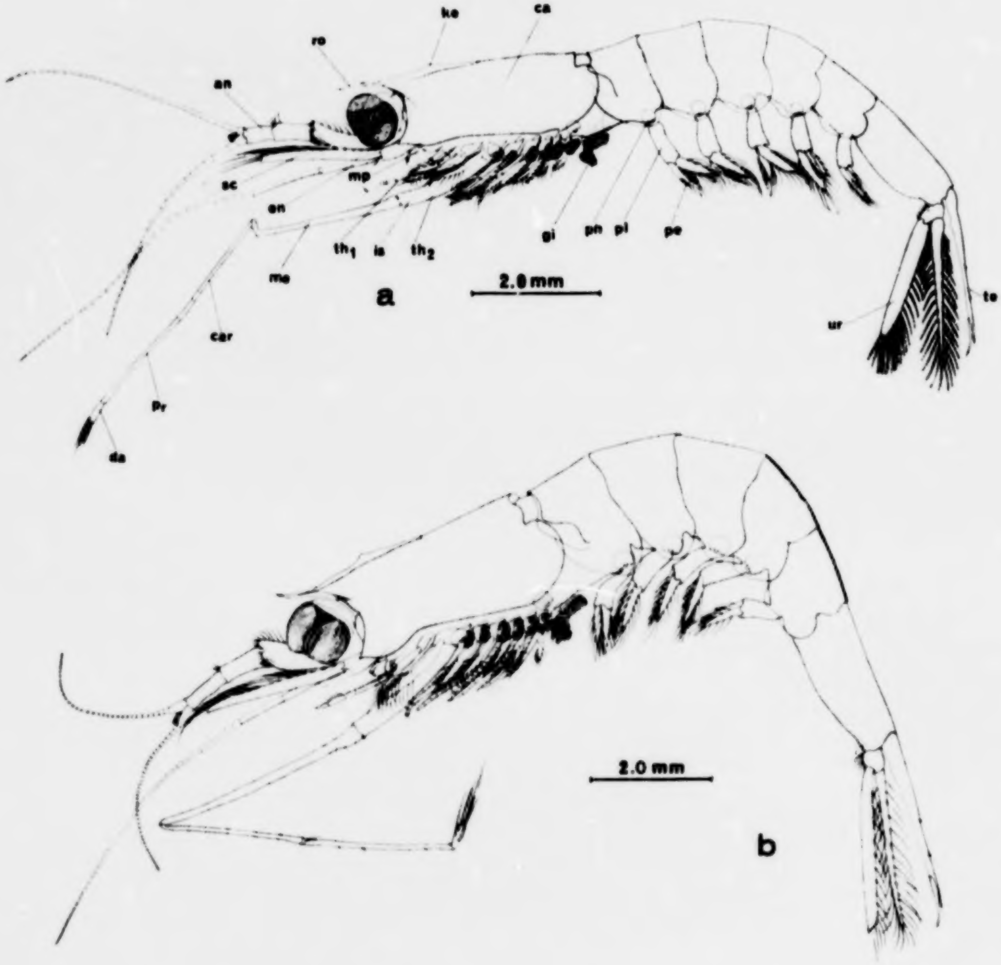


FIGURE 1.—*a*. *Nematoscelis atlantica*, male (length = 13.2 mm; Indian Ocean, position: lat. 28°08′S, long. 66°09′E); *b*. *N. microps*, female (length = 16.3 mm; Indian Ocean, position: lat. 10°06′S, long. 41°51′E). *an*, antennule; *ca*, carapace; *car*, carpus of second leg; *da*, dactylus of second leg; *en*, endopod of antenna; *gi*, gill; *is*, ischium of second leg; *me*, merus of second leg; *mp*, mandibular palp; *pe*, petasma; *ph*, photophore; *pl*, pleopod; *pr*, propodus of second leg; *ro*, rostrum; *sc*, scale of antenna; *te*, telson; th_1, first thoracic leg; th_2, second thoracic leg; *ur*, uropod.

The furcilia phase of *Nematoscelis* was defined in Gopalakrishnan (1973) as follows: compound eyes no longer under carapace, but project outside; antenna retains larval natatory function; pleopod becomes functional, each appears first as non-setose rudiment which develops setae at following moult; furcilia, therefore, with different states of development of pleopods. The following key for identifying furcilia larvae to species is based mostly on diagnostic features of the carapace. There are three developmental stages in the furcilia phase.

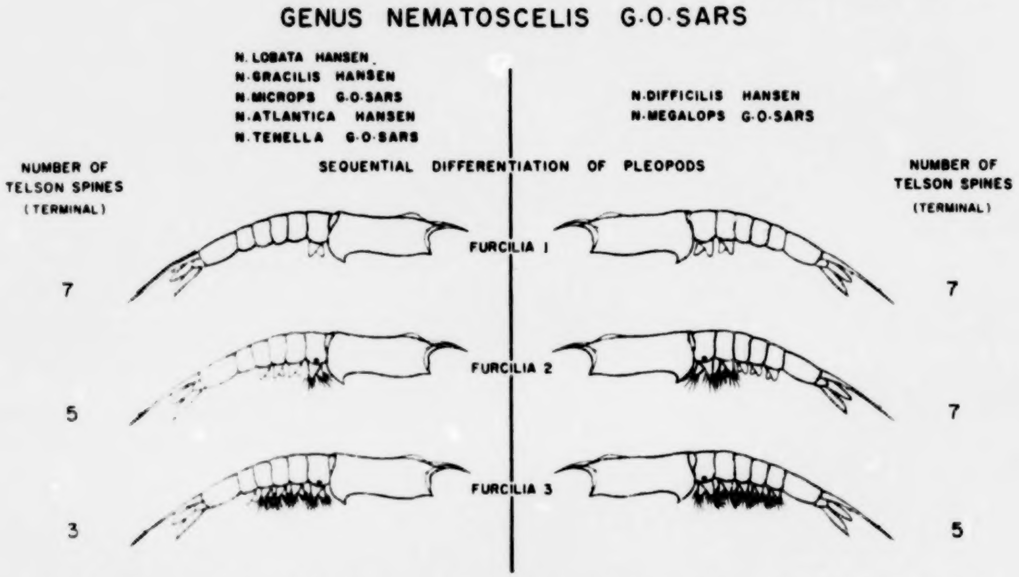

GENUS NEMATOSCELIS G·O·SARS
N. LOBATA HANSEN
N·GRACILIS HANSEN
N·MICROPS G·O·SARS
N·ATLANTICA HANSEN
N·TENELLA G·O·SARS
N·DIFFICILIS HANSEN
N·MEGALOPS G·O·SARS
NUMBER OF TELSON SPINES (TERMINAL)
SEQUENTIAL DIFFERENTIATION OF PLEOPODS
NUMBER OF TELSON SPINES (TERMINAL)
FURCILIA 1
7
7
FURCILIA 2
5
7
FURCILIA 3
3
5

FIGURE 2.–Developmental sequence of differentiation of pleopods and terminal spines of the telson in species of *Nematoscelis* (adapted from Gopalakrishnan 1973).

Key for Identifying Furcilia Larvae of *Nematoscelis*

1a. Each terminal spine of telson with a pair of conspicuous lateral subspines (Figure 3A,a); setules present only above these subspines. F_1 stage with seven terminal spines and one pair of non-setose pleopods; F_2 with five terminal spines, one pair of setose pleopods and three pairs of non-setose pleopods; F_3 with three terminal spines, four pairs of setose pleopods and one pair of non-setose pleopods (Figure 2) 2

1b. Each terminal spine of telson without subspines, but with lateral setules along three-fourths of its length (Figure 3A,b). F_1 stage with seven terminal spines and two pairs of non-setose pleopods; F_2 stage also with seven terminal spines but two pairs of setose pleopods and three pairs of non-setose pleopods; F_3 stage with five terminal spines and five pairs of setose pleopods (Figure 2) 5

2a. Rostrum rectangular with truncated anterior end (Figure 3B,b,c) 3

2b. Rostrum triangular with pointed anterior end (Figure 3B,a,d) 4

3a. Carapace keel very large and hump shaped; rostrum usually curved downwards (Figure 3B,b); length of sixth abdominal segment relatively short and its ventral margin largely convex .... *N. tenella*

3b. Carapace keel small, usually triangular shaped (Figure 3B,c), ventral margin of sixth abdominal segment not convex .... *N. gracilis*

4a. Rostrum broad and stough, keel large and platelike; carapace compressed anteroposteriorly (Figure 3B,a) .... *N. microps*

4b. Rostrum elongate and slender; keel less conspicuous (Figure 3B,d) .... *N. atlantica*

5a. Rostrum broad, thick and triangular (Figure 3B,e) .... *N. megalops*

5b. Rostrum slender and narrow (Figure 3B,f) .... *N. difficilis*

Furcilia larvae of *N. atlantica* and *N. lobata* are difficult to separate. More samples are necessary to complete the larval description of *N. lobata*. This species is known to occur only in the semi-isolated

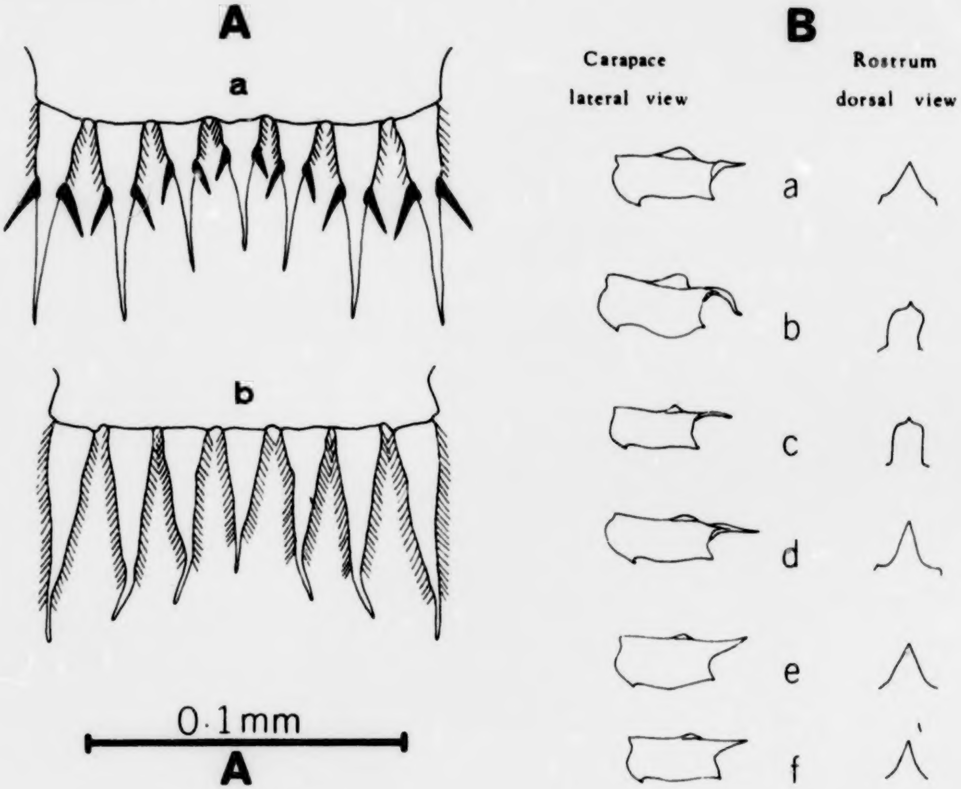


FIGURE 3.–*A*, terminal spines on larval telson: *a*, *Nematoscelis gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, and *N. lobata*; *b*, *N. difficilis* and *N. megalops*. *B*, carapace and rostrum of furcilia larvae of *Nematoscelis*: *a*, *N. microps*; *b*, *N. tenella*; *c*, *N. gracilis*; *d*, *N. atlantica*; *e*, *N. megalops*; *f*, *N. difficilis*.

Sulu and Celebes seas in the region of the Indo-Australian Archipelago (Gopalakrishnan 1974). The distribution of *N. atlantica* appears not to extend into this area. Within each species, the body sizes of metanauplii ranged from 0.8 to 1.0 mm. However, body size differences among all species became apparent from the first calyptopis stage onwards (Table 1). It is at this stage that the larvae start feeding (Gopalakrishnan 1973). Evidently *N. tenella* larvae are the smallest, and *N. megalops* the largest. Length measurements of furcilia larvae also show size differences among

TABLE 1.–Body lengths (mm) of calyptopis stages of *Nematoscelis*. (Medians were based on 10 to 36 individuals of each species for each stage.)

	Stage 1		Stage 2		Stage 3	
Species	Median	Range	Median	Range	Median	Range
N. gracilis	1.4	1.3-1.4	2.1	2.0-2.2	2.6	2.5-2.7
N. microps	1.4	1.3-1.4	2.0	2.0-2.1	2.7	2.6-2.8
N. atlantica	1.5	1.4-1.5	2.2	2.1-2.3	2.8	2.6-2.9
N. tenella	1.2	1.2-1.3	1.8	1.7-1.9	2.5	2.4-2.7
N. megalops	1.6	1.5-1.7	2.4	2.1-2.5	3.2	2.9-3.3
N. difficilis[1]	1.4	1.3-1.5	2.0	1.9-2.1	2.8	2.2-2.8

[1] Data taken from Gopalakrishnan (1973).

TABLE 2.–Body lengths (mm) of furcilia stages of six species of *Nematoscelis*. (Medians were based on 6 to 20 individuals of each species for each stage.)

Species	Stage 1		Stage 2		Stage 3	
	Median	Range	Median	Range	Median	Range
N. gracilis	2.8	2.6-3.0	3.0	2.9-3.4	3.3	3.2-3.5
N. microps	2.9	2.6-3.1	3.2	3.0-3.3	3.5	3.3-3.5
N. atlantica	3.4	3.2-3.5	3.9	3.9-4.1	4.3	4.2-4.5
N. tenella	2.7	2.6-2.9	3.2	3.1-3.3	3.5	3.5-3.6
N. megalops	3.7	3.6-4.0	4.3	4.2-4.3	4.8	4.7-5.0
N. difficilis[1]	3.1	2.7-3.2	3.5	3.4-3.7	3.9	3.6-4.2

[1] Data taken from Gopalakrishnan (1973).

species (Table 2). Between the species pair *N. megalops* and *N. difficilis*, there is a significant size difference during both the calyptopis and furcilia stages.

Juveniles of all species of *Nematoscelis* are identified on the basis of their morphological similarities to adults, especially in such characters as the carapace, the rostrum, and the eye. During the juvenile stages of *N. tenella*, the carapace becomes elongate and narrow as in adults; the dorsal keel on the carapace elongates anteriorly and posteriorly; the broad and curved larval rostrum becomes short and pointed; and the larval eye develops narrow upper and lower lobes (in the adult eye only the lower lobe remains narrow). These diagnostic features help to distinguish juveniles of *N. tenella* from similar stages of other species.

The propodus of the first thoracic leg (maxilliped) is a useful character to identify juveniles, as it is in adults. Although the number of setae on the propodus of this leg is fewer in juveniles than in adults, it is possible to examine the differences in the "style" of setation among juveniles of *Nematoscelis*. For example, in adults of *N. gracilis* there are two rows of setae on the propodus of the maxilliped (Figure 6c); in the juvenile stage this segment develops at least one seta from each position of these two rows. In *N. atlantica* the same segment has only one row (marginal) of setae in adults, and in juveniles at least one seta is present at the position of this marginal row. This difference in the style of setation can be used to distinguish *N. gracilis* and *N. atlantica* juveniles. The propodus of the maxilliped of *N. microps* also has one row of marginal setae, but its inner margin is convex; the carpus of this appendage is shorter than its propodus. The prominent dorsal keel on the carapace is a good diagnostic feature of *N. microps* juveniles.

Nematoscelis G. O. Sars—Generic Characters

The shape of the rostrum variable in males and females; eyes large and bilobed; the peduncle of the first antenna slender in females and thicker in males. Dactylus of the first thoracic leg (maxilliped) triangular, flattened and furnished with comblike setae on its inner lateral margin. The second pair of legs greatly produced and with spines on the distal segment or on both the penultimate and the distal segments. The endopod of the seventh leg biarticulate in the female, lacking in the male. Eighth leg a simple setose plate. All the four processes–proximal, terminal, lateral, and spine-shaped process–present in the petasma; the spine-shaped process always straight and the lateral without any hooks.

Key for Identifying Adult Species of *Nematoscelis*

The following key is adopted from Hansen (1910, 1912), Boden (1954), Boden et al. (1955), and Mauchline and Fisher (1969). It is modified to include additional information:

1a. Second pair of thoracic legs with long spines from both terminal segment (dactylus) and distal end of propodus. Third to sixth thoracic legs with three segments beyond knee. Maxillule with well-developed pseudexopod. Basis of maxilla bilobed. Ventrolateral spine on coxa of antenna greatly produced (Figure 4A,e,f). Carapace with conspicuous cephalic ridge (Figure 5f,g). Eyes large (Figure 4B,e,f). Propodus of first thoracic leg with setae arranged in three rows (Figure 6e,f). Proximal process of petasma with serrations in two rows (Figure 7a,b) 2

1b. Second pair of thoracic legs with long spines from terminal segment (dactylus) only. Third to fourth thoracic legs with only two segments beyond knee, and fifth and sixth with only one. Maxillule without a pseudexopod. Basis of maxilla with one lobe only. Ventrolateral spine on coxa of antenna small or greatly reduced (Figure 4A,a-d). Cephalic ridge on carapace absent or inconspicuous (Figure 5a-e). Eyes relatively small (Figure 4B,a-d). Propodus of first leg with setae arranged in one or two rows (Figure 6a-d). Proximal process of petasma without serrations, or when present in one row only (Figures 7c and 8) 3

2a. Proximal process of petasma reaching almost middle of serrated margin of terminal process (Figure 7a). Serrated part of terminal process slightly curved towards median lobe. Propodus of first leg usually with six setae in outer (dorsal) row and five in middle row .... *N. megalops*

2b. Proximal process reaching much beyond middle of distal part of terminal process (Figure 7b). Distal end of terminal process greatly curved towards median lobe, reaching slightly over distal end of proximal process. Propodus of first leg usually with five setae in dorsal row and four in middle row .... *N. difficilus*

3a. Propodus of first thoracic leg with setae arranged in two separate rows (Figure 6c,d). Lateral process of petasma much longer than both terminal and spine-shaped processes (Figures 7c and 8a). Distal end of lateral process serrated. 4

3b. Propodus of first thoracic leg dorsoventrally flattened and furnished with setae in one row only (Figure 6a,b). Lateral process of petasma much smaller than both terminal and spine-shaped processes (Figure 8b-d). No serrations on lateral process or any other processes of petasma 5

4a. Ventrolateral spine on coxa of antenna highly reduced to a hump (Figure 4A,d). Lower part of eye much smaller than upper part (Figure 4B,d). A long seta projecting from dorsal surface of dactylus of first thoracic leg (Figure 6d). Distal end of lateral process always reaching beyond distal end of proximal process (Figure 8a) .... *N. tenella*

4b. Ventrolateral spine on coxa of antenna not reduced to a hump (Figure 4A,a). Lower part of eye larger than or nearly equal to upper part (Figure 4B,a). No seta on dorsal surface of dactylus of first thoracic leg (Figure 6c). Distal end of lateral process not reaching beyond distal end of proximal process (exception: "old forms" from the Pacific Ocean to be discussed in a later section) (Figure 7c) .... *N. gracilis*

5a. Upper part of eye slightly narrower than lower part (Figures 4B,b and 9c). Propodus of first thoracic leg with less convex inner margin (Figure 6b and 9d). Keel on carapace less prominent and without conspicuous hump. Abdominal segments without any elevated dorsal keels. Shapes and relative lengths of processes of petasma as shown in Figure 8c,d. Lengths of propodus and carpus of first leg nearly equal 6

5b. Upper lobe of eye slightly wider than lower lobe; lateral evagination much deeper in upper than in lower lobe (Figure 4B,c). Propodus of first thoracic leg with highly convex inner margin (Figure 6a). Keel on carapace quite prominent and with conspicuous hump (Figures 5c and 1b). Fourth and fifth abdominal segment characterized by less elevated dorsal keels. Carpus of first leg shorter than propodus. Shapes and relative lengths of processes of petasma as shown in Figure 8b. .... *N. microps*

6a. Proximal process thick; terminal process much shorter than both proximal and spine-shaped processes. Lateral process small. Median lobe greatly flattened and broad; its outer and inner margins broadly convex, inner margin forming an acute distal angle with outer margin (Figure 8c). Adult female without lateral denticle on carapace .... *N. lobata*

6b. Proximal process thin, a little shorter than terminal process; lateral process slightly curved toward median lobe, its distal end reaching to or almost to distal end of proximal process (Figure 8d). Adult female with lateral denticle on carapace .... *N. atlantica*

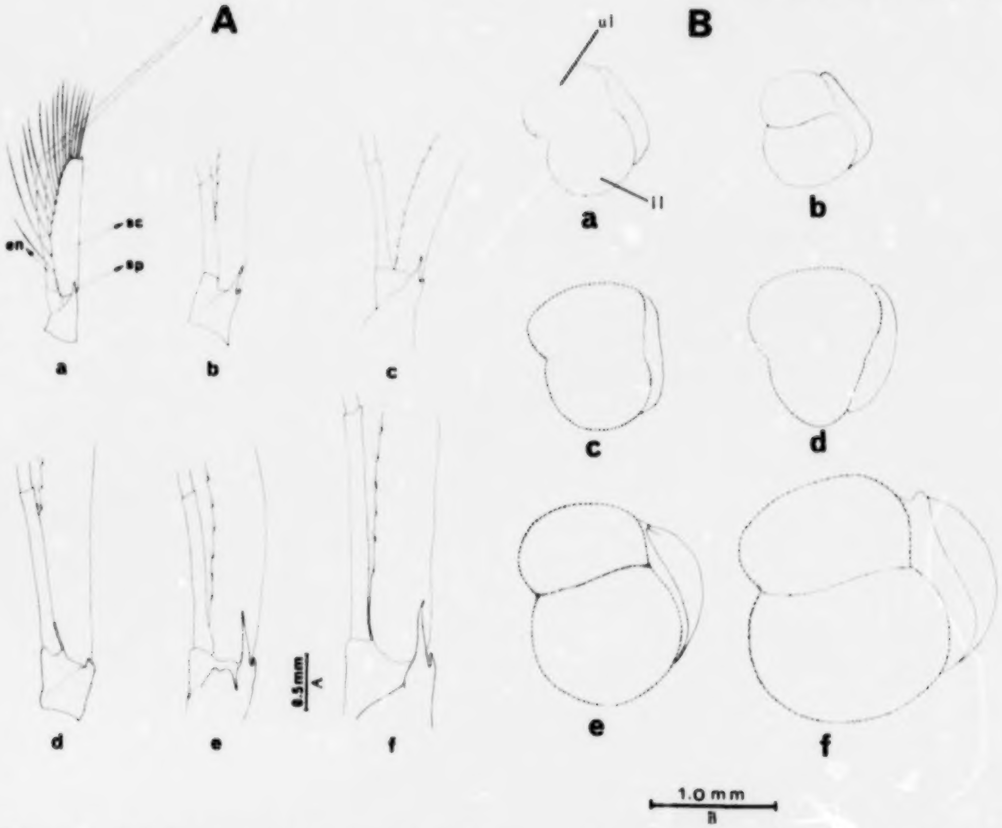


FIGURE 4.--*A*, antenna (ventral view) and *B*, eye (lateral view) of *Nematoscelis*: *a*, *N. gracilis*; *b*, *N. atlantica*; *c*, *N. microps*; *d*, *N. tenella*; *e*, *N. difficilis*; *f*, *N. megalops*. *en*, endopod; *sc*, scale; *sp*, spine on proximal segment of protopod; *ul*, upper lobe; *ll*, lower lobe.

The present study shows that there are two distinct forms in *Nematoscelis gracilis*. They are distinguished as ecophenotypes and are referred to here as the "old form" and the "new form." The old form is identical in morphological characters with the typical form described by Hansen (1910) from the waters of the Indo-Australian Archipelago, and the new form is distinguished from the typical form on the basis of morphological differences on the proximal process of the petasma. There is also an apparent size difference between the two forms: Body length of the old form is significantly larger than that of the new form (cf. Figure 5a,b). The upper lobe of eye in the new form is slightly narrower than that in the old form. Both forms are distinguishable only as adults. The old form occurs mostly in the northern section of the tropical Indo-Pacific subregion and has maximum abundance in the oxygen-poor waters of the Arabian Sea, Bay of Bengal, and eastern tropical Pacific Ocean. The new form occurs in the region of the South Equatorial Current. Along the equatorial zone, where the two forms overlap, an "intermediate" of the two forms, with regard to the length of the proximal process of petasma, is also encountered. Geographical distributions of these forms are described in Gopalakrishnan (1974). There are apparent morphological differences between the old forms of the Indian and Pacific oceans. The following key is prepared for identifying the forms of *N. gracilis*:

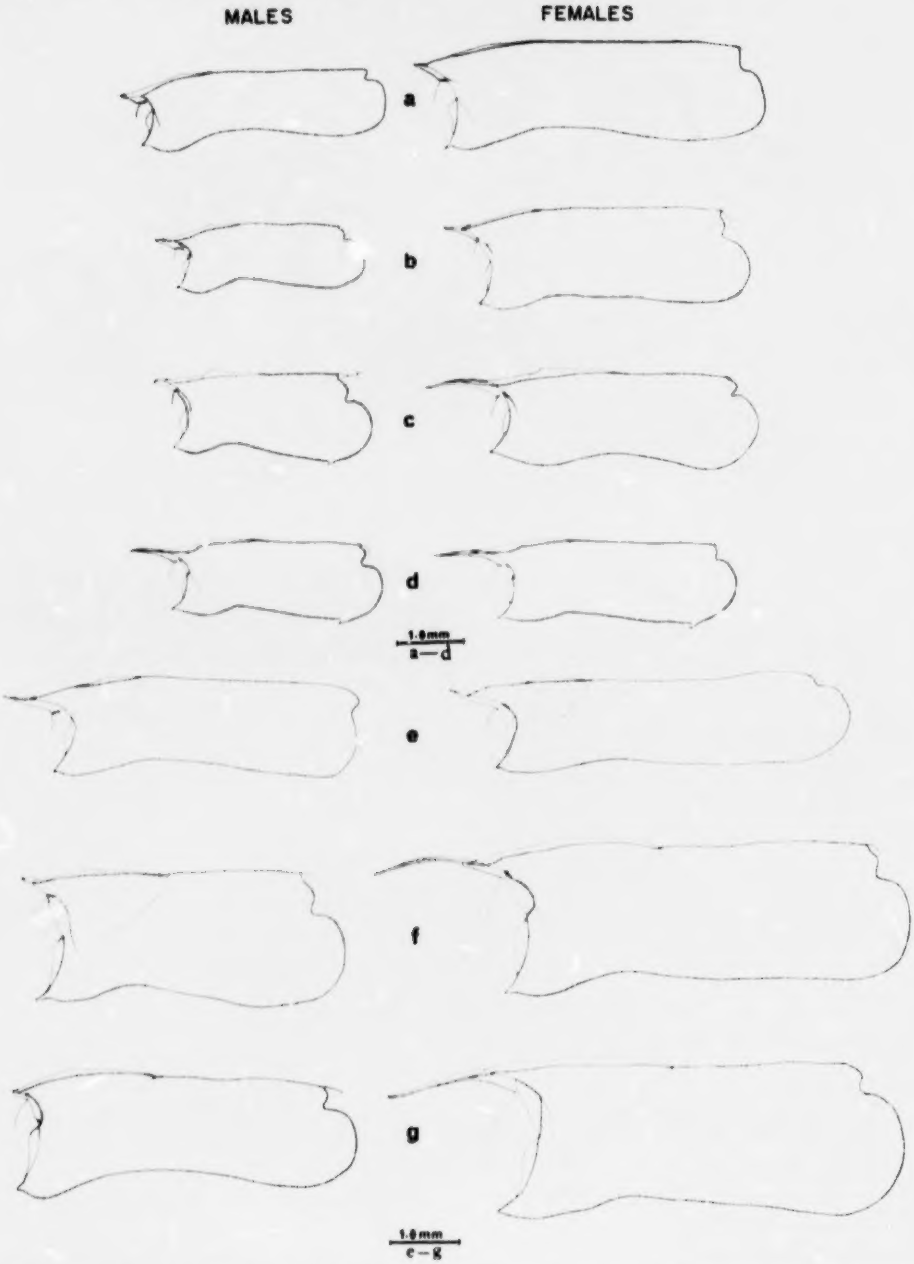


FIGURE 5.—Carapace of *Nematoscelis*: *a*, *N. gracilis* "old form" (length: male = 15.1 mm, female = 16.9 mm); *b*, *N. gracilis* "new form" (length: male = 11.7 mm, female = 15.0 mm); *c*, *N. microps* (length: male = 15.3 mm, female = 17.0 mm); *d*, *N. atlantica* (length: male = 12.9 mm, female = 13.7 mm); *e*, *N. tenella* (length: male = 18.0 mm, female = 19.1 mm); *f*, *N. difficilis* (length: male = 19.0 mm, female = 23.4 mm); *g*, *N. megalops* (length: male = 21.7 mm, female = 25.2 mm).

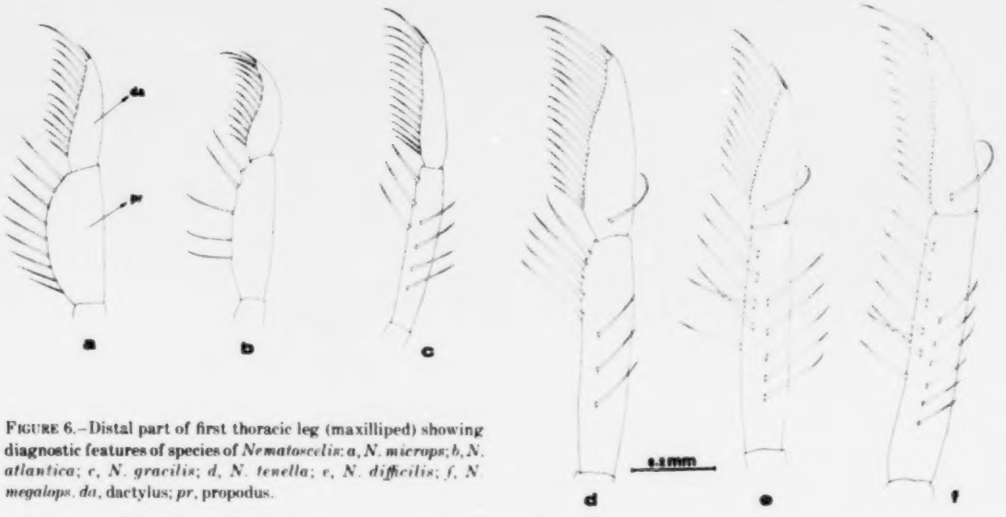


FIGURE 6.–Distal part of first thoracic leg (maxilliped) showing diagnostic features of species of *Nematoscelis*: *a*, *N. microps*; *b*, *N. atlantica*; *c*, *N. gracilis*; *d*, *N. tenella*; *e*, *N. difficilis*; *f*, *N. megalops*. *da*, dactylus; *pr*, propodus.

i. Distal end of lateral process always reaching far beyond distal end of proximal process; proximal process strongly serrated (average number of teeth 10) (Figure 7c) .... Pacific old form

ii. Distal end of proximal process always reaching beyond distal end of lateral process, but not reaching distal end of median lobe; proximal process moderately serrated (average number of teeth 6) (Figure 7c) .... Indian old form

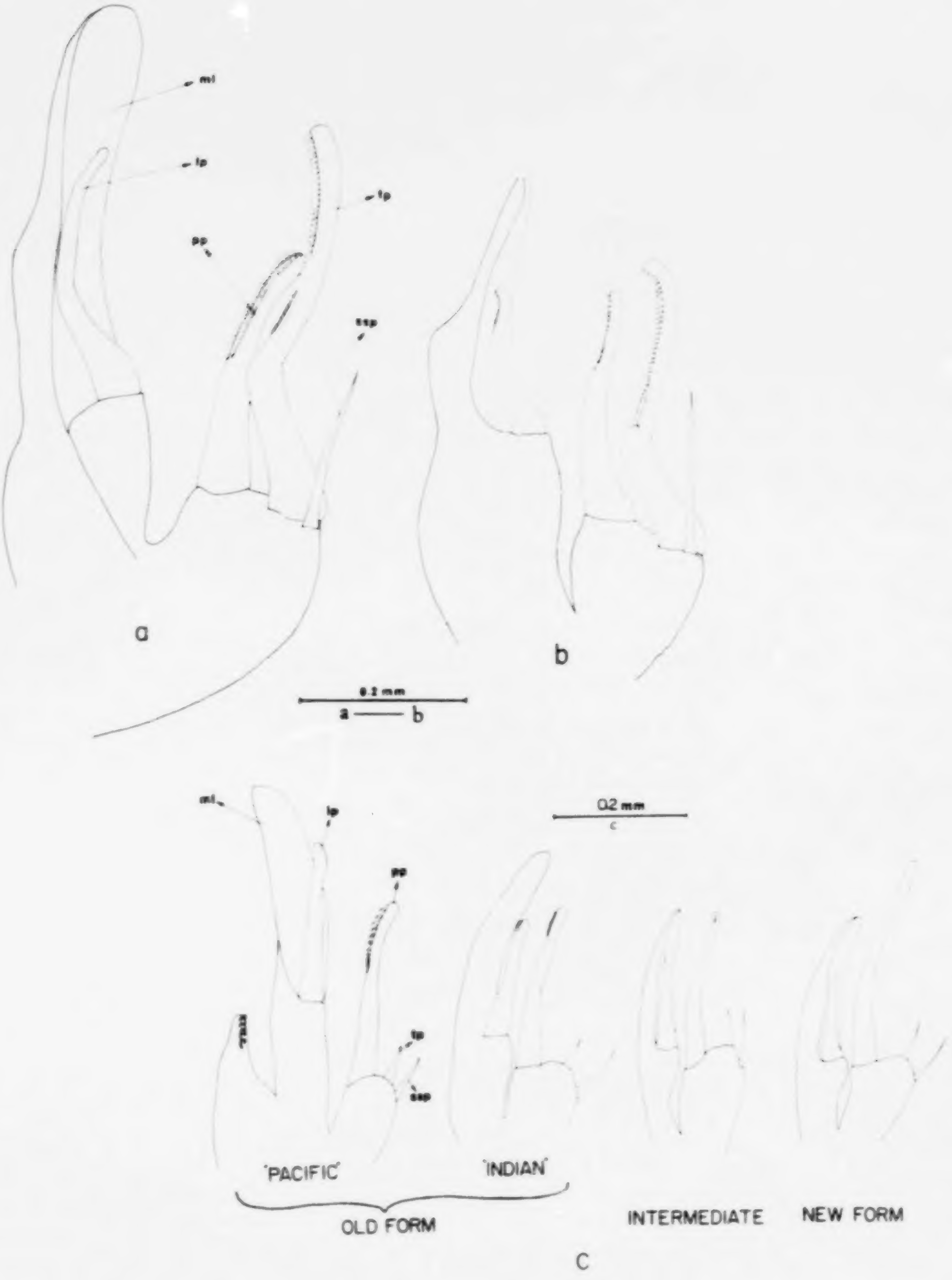
iii. Proximal process extremely long, reaching far beyond distal end of median lobe. Proximal process without any serrations (Figure 7c).. new form

iv. Proximal process much longer than lateral process, its distal end reaching as far as distal end of median lobe. Proximal process slightly serrated (average number of teeth 3) (Figure 7c) .... intermediate of old and new forms

The two forms of *N. gracilis* can also be separated with certainty by plotting the ratio of the proximal process to the median lobe of petasma against carapace length (Figure 10). The intermediate forms represent the presumed intergradation of new and old forms, although they appear to be much closer to the old form than to the new form with respect to this character. The difference in body lengths between old forms of the Indian and Pacific oceans is also apparent from this figure. Table 3 shows results of an analysis of covariance on proximal process of the petasma and carapace length of *N. gracilis* old and new forms. Length of the proximal process of petasma of the old form is significantly different statistically from that of the new form. Body lengths of the old forms in the Pacific and Indian oceans are significantly different statistically. Both intermediate and new forms are smaller than the old forms. Lengths of both the median lobe and lateral process are also different in these forms.

Of the 55 morphological characters measured, many showed statistically significant differences between species pairs. For example, the following characters of *N. gracilis* were different from those of *N. microps*: basal length of keel; length of carpus of first thoracic leg; lateral length of carapace; length of carapace between apex of keel and its posterolateral margin; length of carapace between apex of keel and point above photophore on seventh thoracic segment; distance between photophore on coxa of second thoracic leg and photophore on coxa of seventh thoracic leg; lengths of

FIGURE 7.–Petasmae of *Nematoscelis*: *a*, *N. megalops*; *b*, *N. difficilis*; *c*, *N. gracilis* forms. *lp*, lateral process; *ml*, median lobe; *pp*, proximal process; *ssp*, spine-shaped process; *tp*, terminal process.


ml
lp
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'PACIFIC'
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OLD FORM
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NEW FORM
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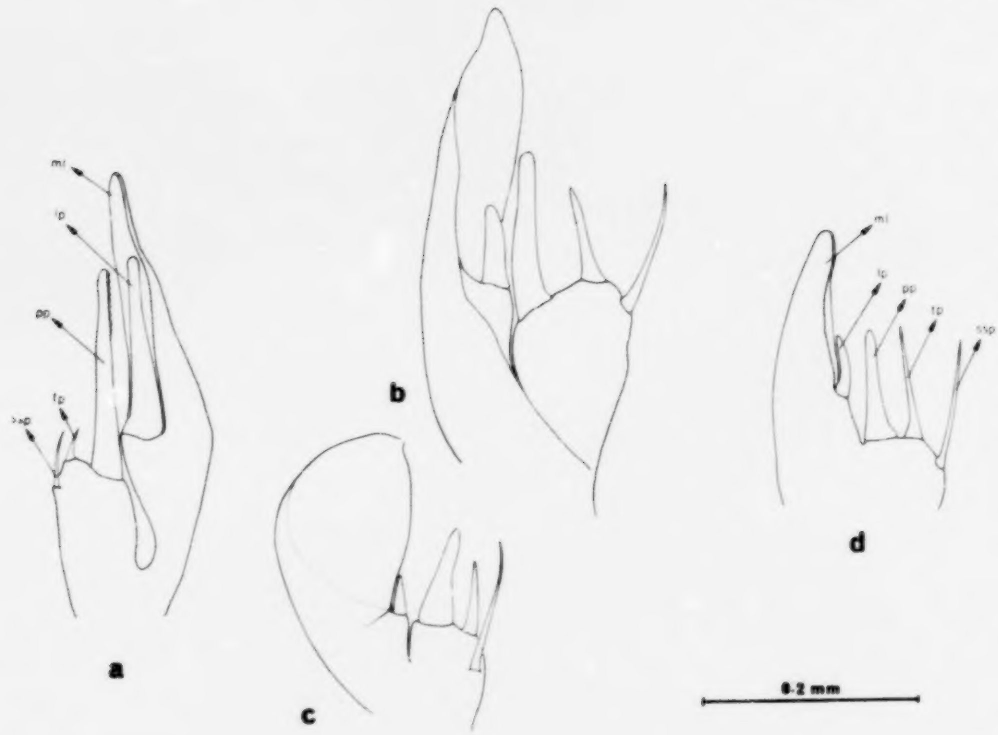

FIGURE 8.–Petasmae of *Nematoscelis*: *a*, *N. tenella*; *b*, *N. microps*; *c*, *N. lobata*; *d*, *N. atlantica*. *lp*, lateral process; *ml*, median lobe; *pp*, proximal process; *ssp*, spine-shaped process; *tp*, terminal process.

TABLE 3.–Analysis of covariance on proximal process of the petasma and carapace length of *Nematoscelis gracilis* "old form" (Indian Ocean) and the "new form."

Source	Sum of squares	Degrees of freedom	Mean square	*F* ratio	Probability
Proximal process alone:					
Between means	26.934	1	26.934	$F_{1,58} = 328.463$	<0.0001
Within groups	4.786	58	0.082		
Total	31.720	59			
After accounted for differences in carapace lengths:					
Between means	21.136	1	21.136	$F_{1,57} = 289.534$	<0.0001
Within groups[1]	4.186	57	0.073		
Regression (overall)	6.398	1			
Total	31.720	59			

[1] 0.600 is *within SS* (regression) removed.

spine-shaped process, terminal process, proximal process, and lateral process of petasma; basal width of lateral process of petasma; number of marginal setae on exopod of maxilla; number of setae on second segment of mandibular palp. Similarly, *N. atlantica* and *N. microps* differ as follows: in dorsal length of first abdominal segment; length of keel on carapace; lateral length of sixth abdominal segment; length of carpus of first thoracic leg; width of upper lobe of eye; lateral length of carapace; length of carapace between apex of keel and its posterolateral margin; length

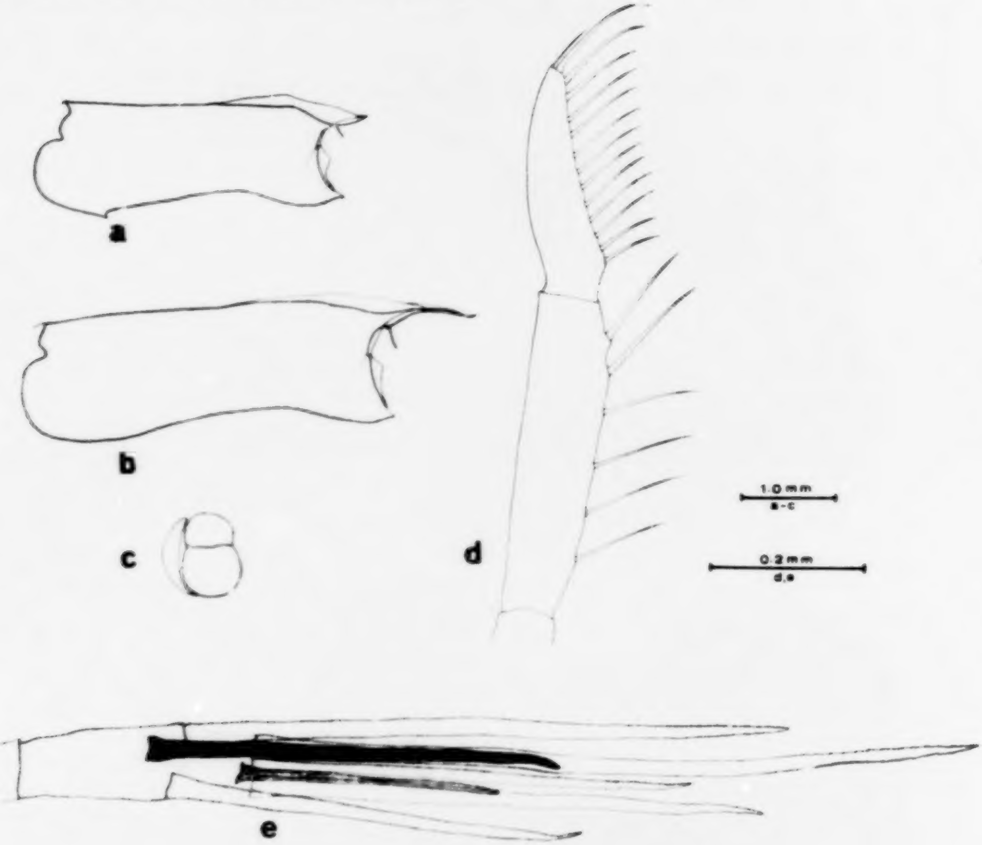

FIGURE 9.–*Nematoscelis lobata*: *a*, male carapace (body length = 12.1 mm); *b*, female carapace (body length = 13.5 mm); *c*, eye; *d*, distal part (propodus and dactylus) of first thoracic leg (maxilliped); *e*, dactylus of second thoracic leg showing arrangement of apical spines.

of carapace between apex of keel and the point above photophore on seventh thoracic segment; distance between photophore on coxa of second thoracic leg and photophore on coxa of seventh thoracic leg; length of proximal process of petasma; basal widths of lateral and proximal processes of petasma.

Nematoscelis tenella differs from other species in length of carpus of second thoracic leg, width of lower lobe of eye, lengths of merus and propodus of second thoracic leg, length of lateral spine of protopod of antenna, lengths of spine-shaped process and terminal process of petasma and basal widths of spine-shaped process and terminal process of petasma.

The lengths of the spine-shaped process and proximal process of the petasma and number of marginal setae on the pseudexopod of the maxillule of *N. difficilis* are different from *N. megalops*. The species pair *N. difficilis*-*N. megalops* differs from other species in the following characters: basal length of keel; length of scale of antenna; lengths of carpus, dactylus, and longest spine on distal end of second leg; lengths of ischium and merus of first thoracic leg; vertical length and width of lower lobe of eye; dorsal length of first abdominal segment; length and basal width of terminal process of petasma; number of marginal setae on exopod of maxilla, endopod and pseudexopod of maxillule, and on

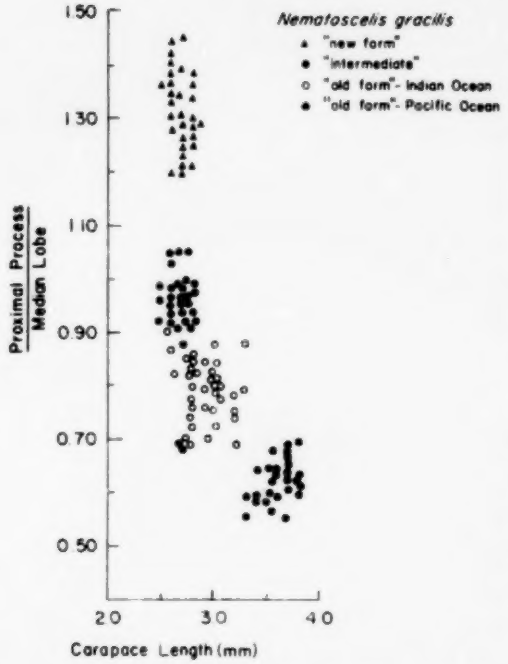

FIGURE 10.–*Nematoscelis gracilis* forms: ratio of proximal process to median lobe of petasma plotted against carapace.

propodus of first thoracic leg; number of marginal spine on lacina externa of maxillule; number of setae on second segment of mandibular palp.

Sexual Dimorphism in *Nematoscelis*

Sexual dimorphism in euphausiids was best documented by Hansen (1910, 1912). Einarsson (1942) and Nemoto (1966) provided further details. The most sexually dimorphic characters are: the lateral denticle, keel, and rostrum of carapace; antennule; eyes; sixth and seventh thoracic legs; first and second abdominal pleopods; preanal spine.

The states of the lateral denticle, keel, and rostrum in both sexes of *Nematoscelis* are illustrated in Figure 5. The carapace and rostrum are shorter in males than in females. The rostrum in the male is rarely variable; in the female it is always long and slender, except in *N. gracilis* and *N. tenella*. The lateral denticle is absent in all species except in males of *N. microps* and both sexes of *N. atlantica*. McLaughlin (1965) reported the occurrence of this denticle in both subadult and adult stages of *N. difficilis* caught from the northeastern Pacific Ocean. In the present study, the lateral denticle on the carapace was found only in immature specimens of this species, but not in adults. These individuals were collected from the North Pacific Drift and California Current areas. No sexual dimorphism was observed in the shape of eyes in *Nematoscelis*. The antennular peduncle in males has the two distal segments much thicker than in females; the second segment somewhat shorter and the third segment much shorter than in females (Figure 11A,a,b). The lower flagellum of the antennule has the basal segment much thickened in males and furnished with tufts of sensory setae. In *N. gracilis* males, the proximal part of this flagellum bends downward so as to accommodate the enlarged basal segment (Figure 11A,a).

Sexual dimorphism in abdominal photophores is characteristic of *Nematoscelis*. Einarsson (1942) pointed out a few examples of enlargements of abdominal photophores in this genus. James (1973) reported the existence of this feature in the North Atlantic species of *N. tenella*, *N. atlantica*, and *N. microps*. In the course of examining the material from all oceans, certain interspecific differences of photophore enlargement have become evident. In females of all species of *Nematoscelis*, the photophores on each of the first four abdominal segments are more or less alike in size and shape (Figure 1b). However, in males, one or more of these photophores often show considerable enlargement. The patterns of this enlargement appear to be consistent, species specific, and therefore of diagnostic value.

Associated with photophore enlargement is the occurrence of paired chitinous saddle-shaped plates on the dorsal side of the abdominal segment anterior to that in which the photophore is enlarged (Figure 11B). Types of photophore enlargement in species of *Nematoscelis* are shown in this figure. In the Indian Ocean, *N. gracilis* males have the first abdominal photophore enlarged and lack chitinous plates on the dorsal side of the abdomen. *Nematoscelis microps* males have the second photophore enlarged and either with a dorsal hump (Figure 11B,b) or paired chitinous plates on the dorsal side of the first abdominal segment. Taniguchi (1966) reported occurrence of this hump on *N. microps* collected from the northeastern Indian Ocean. Humped males of this species are frequently found in the tropical

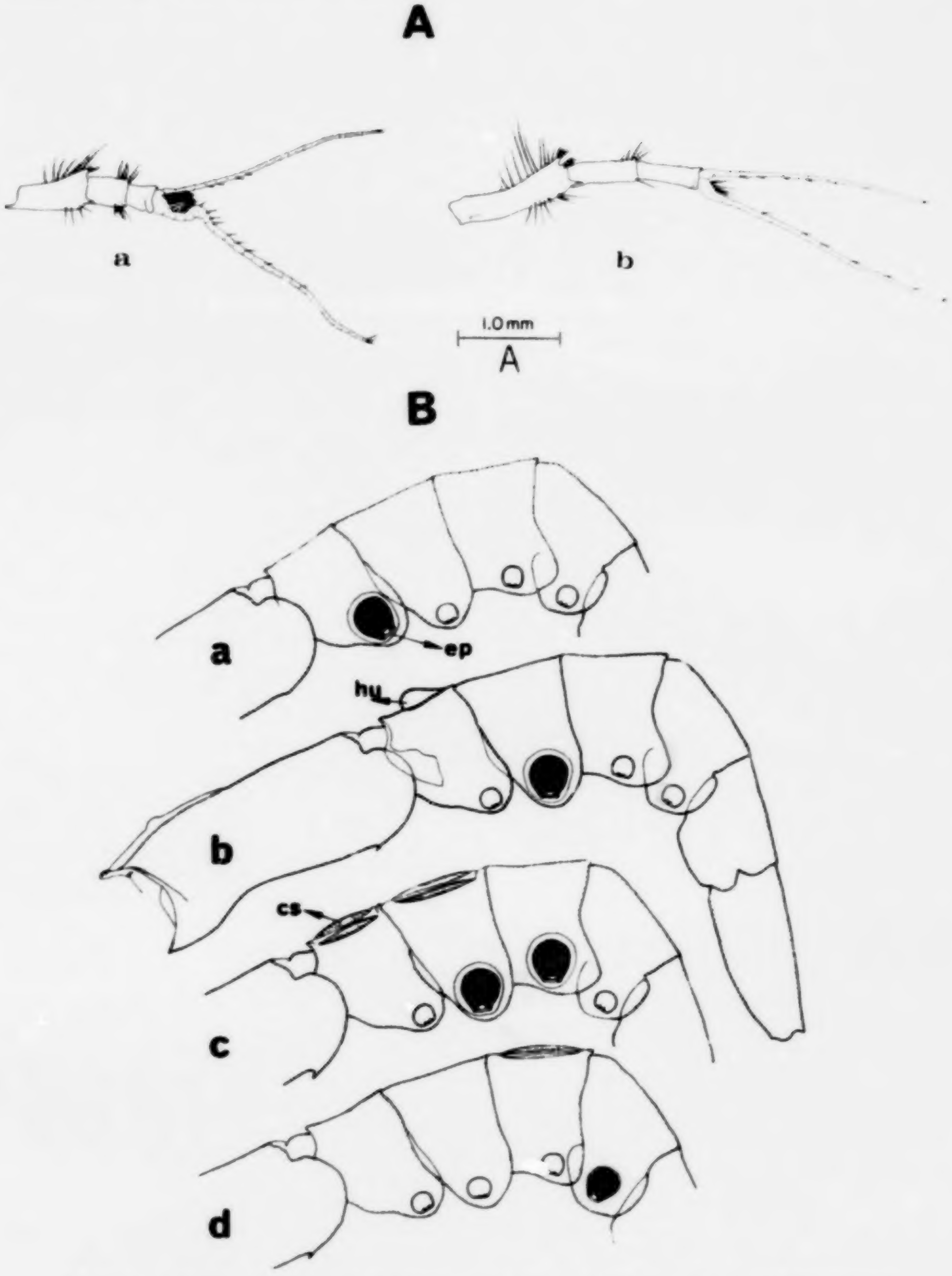

FIGURE 11.–*A*, dimorphic antennule of *Nematoscelis gracilis*: *a*, male; *b*, female. *B*, enlarged photophores of *Nematoscelis* males: *a*, *N. gracilis* forms; *b*, *N. microps*; *c*, first form of *N. tenella* and *N. atlentica*; *d*, second form of *N. tenella* and *N. atlantica*. *ep*, enlarged photophore; *hu*, dorsal hump; *cs*, chitinous "saddle."

Indo-West Pacific subregion. *Nematoscelis microps* males with paired chitinous plates on the first abdominal segment occur mostly in the tropical regions of the Pacific, Atlantic, and Indian oceans. James (1973) found this form of *N. microps* occurring in the northeast Atlantic south of lat. 20°N. Adult males of *N. microps* without any photophore enlargement were also found in all oceans, but they occur mostly in the subtropical regions.

Nematoscelis tenella and *N. atlantica* males have two forms of photophore enlargement (Figure 11B,c and 11B,d): one form has the second and third photophores enlarged along with the presence of saddle-shaped paired plates on the dorsal side of both the first and second abdominal segments; the other form shows photophore enlargement on the fourth abdominal segment along with paired plates on the third abdominal segment. These two species occur together in the northern and southern subtropical provinces of all oceans. They also occur together in the tropical regions of the Atlantic Ocean. When the two species occur in the same geographical area, the males of both species do not show the same pattern of photophore enlargement. In such cases the pattern of photophore enlargement is as follows:

Species	*Subtropics*	*Tropics*
Nematoscelis tenella	First form*	Second form**
Nematoscelis atlantica	Second form**	First form*

*Saddle-shaped plates on first and second abdominal segments and photophore enlargements on second and third.

**Saddle-shaped plates on third abdominal segment and photophore enlargement on fourth.

Nematoscelis atlantica does not occur in the tropical regions of the Pacific and Indian oceans; *N. tenella* males in this region have the second form of photophore enlargement. There is no clear evidence of photophore enlargement in *N. difficilis* and *N. megalops*.

Even though a pattern of photophore enlargement appears to be characteristic of each species, not all mature males show this feature. When present, about 60-80% of the males in each sample had specific patterns of photophore enlargement as described above. Structure of the petasma of these forms did not differ from the typical forms. One is tempted to speculate on the evolutionary significance of this feature. The occurrence of the dorsal chitinous plate and the enlargement of the photophore in adult males may have some joint functional importance, probably related to sexual behavior. Evidently, these abnormal conditions are not random phenomena; patterns are of specific nature and have clear association with sexual maturity. The fact that *N. tenella* and *N. atlantica* do not have the same form of photophore enlargement when they occur together in a geographical area suggests the possible role of these specific patterns in enhancing species recognition for mating.

DISCUSSION

Among the morphological characters of a species, feeding and reproductive structures afford specific features that have diagnostic value. The specificity of the feeding appendages reflects presumed niche specializations. The structural uniqueness in the reproductive system ensures reproductive isolation of the species upon which the biological species concept is founded (Mayr 1942). Therefore, a key based on these characters should be the best in distinguishing individual species. The selection of the maxillliped as a diagnostic character has the advantage that the same key may be used for both sexes. However, it did not prove possible to make such a key for the larva.

The species of *Nematoscelis* can be grouped into two subgroups, one with *N. difficilis* and *N. megalops* and the other with the rest of the five species. The present study has brought out both ecological and systematic evidences to support such a grouping. The sequential development of larval characteristics also suggests phylogenetic differences between the two subgroups. Hansen (1912), using the structure of adult maxillule, proposed a division of *Nematoscelis* into these two groups. A similar division was also made by Mauchline (1967) on the basis of structural differences in the adult maxilla.

When closely related species are partially sympatric, behavioral mechanisms might operate to insure reproductive isolation of the species (Mayr 1966). Usually the presence or absence of intergradation between sympatric populations serve as indicators of interbreeding or reproductive isolation. Presumably, the absence of intergradation between species of *Nematoscelis* occupying the same geographical area suggests reproductive isolation. However, the absence of reproductive isolation between the two forms of *N. gracilis* is probably shown by the occurrence of sexually mature intermediate forms in the overlapping regions of their distribution. The fact that the observed diagnostic feature lies on the reproductive structure would suggest probable genetic separation. Nonetheless, until more is known about the ecology and behavior of these forms, I do not wish to formally describe them as species or subspecies and will consider them ecophenotypes. The pattern of geographical distribution of these forms appears to be correlated with differences in environmental characteristics, particularly the distribution of dissolved oxygen in the water column (Gopalakrishnan 1974).

Allopatric populations are inferred to have undergone reproductive isolation if they are morphologically distinct and do not show any overlap in their diagnostic features. *Nematoscelis difficilis* and *N. megalops* are allopatric, occupying the northern and southern transitional zones of the Pacific respectively. *Nematoscelis megalops* also occurs in the Atlantic and Indian oceans. On the basis of similarities in the structure of the petasma of *N. difficilis* and *N. megalops*, Karedin (1971) questioned the validity of *N. difficilis*. Brinton (1962) considered them a sibling species pair evolved as a result of complete geographical separation. Although closely related, there are certain morphological features that distinguish one species from the other. Both quantitative and qualitative features of the reproductive system, the petasma in this case, indicate significant differences. The petasmae of *N. megalops* in the South Pacific, South and North Atlantic, and South Indian oceans show no apparent structural difference. These populations are probably in continuum facilitating gene exchange. (Communication between North and South Atlantic populations of *N. megalops* appears possible from the fact that only in this ocean does the characteristically subtropical species *N. atlantica* occur also in the tropics. This suggests that in the Atlantic the low-latitude boundaries of distribution of subtropical species approach the equator, permitting at least occasional north-south communication). The validity of *N. difficilis* can be supported by the fact that this species and *N. megalops* do not overlap geographically in the Pacific Ocean. Both species live in comparable environments (narrow mid-latitude zones) and therefore are probably exposed to similar selection pressures. In such a situation, even though geographical isolation would be complete, morphological differentiation might be slow. In the absence of gene exchange, the populations would be expected to have diverged genetically. The relative lengths and shapes of the median lobe, proximal, terminal, and lateral spines of petasmae of the two species differ, supporting the validity of *N. difficilis*. In Hansen's words (1916) these differences are "certainly so sharp, so important, and so constant that they are sufficient for separating *N. difficilis* from *N. megalops*."

The *N. atlantica* population in the North Pacific is spatially separated from its counterpart in the South Pacific Ocean. No morphological distinctness was evident in this population, although it may prove to be genetically separate from others. *Nematoscelis lobata* is endemic to the Sulu and Celebes seas in the Indo-Australian Archipelago (Gopalakrishnan 1974). According to Hansen's (1916) description, this species is very similar to *N. microps*. The present study indicates that in many morphological characters *N. lobata* is more related to *N. atlantica* than to *N. microps*. *Nematoscelis lobata* and *N. atlantica* are allopatrically distributed and have probably acquired characters which promote or guarantee their reproductive isolation.

The observed differences in the structure of the first thoracic leg (maxilliped) of species of *Nematoscelis* indicate presumed specialization in feeding habits. All species of this genus are recognized to be omnivores. From a comparison of the first thoracic legs, it appears that species would be expected to show different types of feeding. *Nematoscelis microps*, *N. atlantica*, and *N. lobata*, having marginal setae (one row) on their propodus of the first thoracic legs, may be better fitted for filtering a large proportion of phytoplankton in their food, whereas *N. difficilis* and *N. megalops*, having three rows of setae on the propodus of the first leg, may select more animal food. In this respect *N. gracilis* and *N. tenella* are intermediate. Existing information on the gut contents of species of *Nematoscelis*, e.g., Nemoto (1967) and Weigmann (1970), is inadequate to substantiate this.

ACKNOWLEDGMENTS

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LITERATURE CITED

BODEN, B. P.

1954. The euphasiid crustaceans of southern African waters. Trans. R. Soc. S. Afr. 34:181-243.

BODEN, B. P., M. W. JOHNSON, AND E. BRINTON.

1955. The Euphausiacea (Crustacea) of the north Pacific. Bull. Scripps Inst. Oceanogr., Univ. Calif. 6:287-400.

BRINTON, E.

1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8:51-269.

EINARSSON, H.

1942. Notes on Euphausiacea I-III. On the systematic value of the spermatheca, on sexual dimorphism in *Nematoscelis* and on the male in *Bentheuphausia*. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 106:263-286.

GOPALAKRISHNAN, K.

1973. Developmental and growth studies of the euphausiid Nematoscelis difficilis (Crustacea) based on rearing. Bull. Scripps Inst. Oceanogr., Univ. Calif. 20:1-87.

1974. Zoogeography of the genus *Nematoscelis* (Crustacea, Euphausiacea). Fish. Bull., U.S. 72:1039-1074.

GORDON, I.

1955. Importance of larval characters in classification. Nature (Lond.) 176:911-912.

HANSEN, H. J.

1910. The Schizopoda of the Siboga expedition. Siboga Exped. 51(37):1-123.

1911. The genera and species of the order Euphausiacea, with account of remarkable variation. Bull. Inst. Oceanogr. (Monaco) 210:1-54.

1912. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U.S.N., commanding. 27. The Schizopoda. Mem. Mus. Comp. Zool. Harvard Coll. 35(4):175-296.

1916. The Euphausiacean crustaceans of the "Albatross" Expedition to the Philippines. [Sci. Results Philippine Cruise Fish. steamer "Albatross," 1907-1910. No. 33.] Proc. U.S. Natl. Mus. 49:635-654.

JAMES, P. T.

1973. Distribution of dimorphic males of three species of *Nematoscelis* (Euphausiacea). Mar. Biol. (Berl.) 19:341-347.

KAREDIN, E. P.

1971. On the similarity between *Nematoscelis megalops* G. O. Sars, 1885, and *N. difficilis* Hansen, 1911 (Euphausiacea, Crustacea) and on the substantiation for the isolation of *N. difficilis* Hansen into a separate species. [Translated from Russian by Edith Roden.] Tikookean. Nauchno-issled. Inst. Rybn. Khoz. I. Okeanogr. (TINRO) 75:121-129.

MAUCHLINE, J.

1967. The feeding appendages of the Euphausiacea (Crustacea). J. Zool. (Lond.) 153:1-43.

MAUCHLINE, J., AND L. R. FISHER.

1969. The biology of euphausiids. Adv. Mar. Biol. 7:1-454.

MAYR, E.

1942. Systematics and the origin of species. Columbia Univ. Press, N.Y., 334 p.

1966. Animal species and evolution. Belknap Press, Camb., Mass., 797 p.

MCLAUGHLIN, P. A.

1965. A redescription of the euphasiid crustacean, *Nematoscelis difficilis* Hansen, 1911. Crustaceana 9:41-44.

NEMOTO, T.

1966. *Thysanoessa* euphausiids, comparative morphology, allomorphosis and ecology. Sci. Rep. Whales Res. Inst., Tokyo 20:109-155.

1967. Feeding pattern of euphausiids and differentiations in their body characters. Inf. Bull. Planktology Jap., 61st Annu. No. 143-160.

RUUD, J. T.

1936. Euphausiacea. Rep. Dan. Oceanogr. Exped. 1908-1910 Mediter. Adjacent Seas 2D6 (Biol.), 86 p.

SARS, G. O.

1883. Preliminary notices on the Schizopoda of H.M.S. Challenger Expedition. Forsch. Vidensk. Selsk. Krist. 7:1-43.

1885. Report on the Schizopoda collected by H.M.S. Challenger during the years 1873-76. Rep. Sci. Res. H.M.S. Challenger 13(37), 228 p.

TANIGUCHI, A.

1966. Abnormal specimens of a euphausiid, *Nematoscelis microps*, collected in the Indian Ocean. Inf. Bull. Planktology Jap. 13:106-107.

WEIGMANN, R.

1970. Zur Okologie und Ernahrungsbidogie der Euphausiaceen (Crustacea) im Arabishen Meer. METEOR Forsch. Ergeb. 5:11-52.

FOOD, ACTIVITY, AND HABITAT OF THREE "PICKER-TYPE" MICROCARNIVOROUS FISHES IN THE KELP FORESTS OFF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Diets, daily activity, and habitat preference were compared between the kelp perch, *Brachyistius frenatus*; the señorita, *Oxyjulis californica*; and the white seaperch, *Phanerodon furcatus*, all of which co-occur in areas of reef and kelp off Santa Barbara, Calif. The kelp perch and señorita often clean ectoparasites off larger host fishes, whereas the white seaperch is a more generalized picker-type microcarnivore.

The kelp perch and señorita, which co-occur in the kelp canopy, showed the least amount of total overlap in resource use, expressed as a combination of individual overlaps in food, activity, and habitat. The señorita had the narrowest breadth of diet but the widest breadth of habitat (within the kelp-bed areas). Señoritas and white seaperch ate mostly bryozoans encrusted on plants, whereas kelp perch ate mostly plankton and other tiny motile prey. As species, neither the kelp perch nor the señorita derives substantial amounts of food from cleaning, although some individual señoritas may. Unlike the two "cleaners," the white seaperch also ate substantial numbers of bottom prey. None of the species forage at night, when all are relatively inactive, and when the señorita actually buries itself in patches of rubble and sand on the reef. The two perches showed the greatest overlap in daytime activity, as measured both by bi-hourly counts of feeding bites in the field and of swimming movements in a laboratory tank.

Fishes that exploit the same class of environmental resources in similar ways may be thought of as forming a "guild" of species having similar ecological roles regardless of their taxonomic affinities (Root 1967). In and about the forests of giant kelp off southern California, fishes that can select relatively small prey from mid-water and from kelp or other surfaces form a foraging guild of "pickers" (cf. Hobson 1971). Hubbs and Hubbs (1954) stressed the fact that two common and taxonomically unrelated pickers have remarkably similar mouth structures and dentitions: the kelp perch, *Brachyistius frenatus*, which is in the primarily temperate family of surfperches Embiotocidae, has evolved the same general type of pointed snout, tiny jaws, and protruding canines that characterize the señorita, *Oxyjulis californica*, and most other members of the primarily tropical family of wrasses Labridae.

Hobson (1971) noted that the habit of cleaning ectoparasites off larger fishes is widespread among the picker-type fishes. Señoritas, kelp perch, and young of another embiotocid, the sharpnose seaperch, *Phanerodon atripes*, are the most consistent "cleaner fishes" of the kelp beds (Limbaugh 1961; Hobson 1971). Compared to some small tropical wrasses (Randall 1958), however, these species are less specialized as cleaners: their cleaning activities are sporadic and/or confined to certain individuals, and so their principal forage must be elsewhere (Hobson 1971).

With this in mind, we compared the diets, daily activity patterns, and habitat preferences of the señorita and kelp perch, which are the principal cleaner fishes in the Santa Barbara area, with those of a more generalized picker, the white seaperch, *P. furcatus*. These three species have been studied off San Diego (Limbaugh 1955; Quast 1968a, b; Hobson 1971). Yet little has been published on their habits and distribution off Santa Barbara. Here the Channel Islands and the east-west oriented coastline protect kelp beds from swells, enabling giant kelp to anchor on low-relief and soft bottoms as well as to high-relief reefs. Also, species with centers of distribution located far to the north are more frequently encountered (Quast 1968a; Ebeling et al. 1971).

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METHODS

Kelp perch, white seaperch, and señoritas were observed in the field and laboratory. Over a 2-yr period, scuba divers spent more than a total of 125 h watching and collecting fish both day and night at depths ranging from 1 to 20 m. Study localities included areas of reef and kelp in the Santa Barbara Channel–off the Santa Barbara mainland and off Santa Cruz Island located across the Channel some 42 km to the south.

Food

During 27 scuba dives made between February, 1971 and March, 1973, we collected a total of 115 kelp perch (measuring 43-142 mm, averaging 103 mm standard length), 111 white seaperch (74-203, 139 mm), and 65 señoritas (110-227, 169 mm). Gut contents were found in and identified from 50 kelp perch, 55 white seaperch, and 53 señoritas. All fish were taken with a small, 15-prong pole spear. Later they were slit ventrally, fixed in 10% Formalin,[1] washed, and preserved in 45% isopropanol. During the analysis, fish were identified by numbered tag only so as to minimize any bias that might result from forehand knowledge of time of collection, etc.

For all three species, the simple, tubular gut, which is "stomachless" in the sense of Chao (1973), was excised, measured, and divided from front to back into three sections of equal length, here arbitrarily called the "fore-," "mid-," and "hindgut," respectively. Fullness of each section was scored subjectively from 1 (empty) to 5 (full and distended). Scores were plotted against time of day. Because fish were sampled throughout the year, their times of collection were seasonally adjusted relative to times of sunrise and sunset as listed in solar tables for the particular dates. Adjusted time of collection, rounded to the nearest 2-h interval, was measured on the relative scale with sunrise arbitrarily set at 0600 h and sunset at 1800 h.

Displayed under a dissecting scope, the contents of the foregut were sorted into broad taxonomic categories of food items, which were segregated in a small, partitioned tray. Then the percent volume of each item in the array was estimated by eye. Estimates were made quickly to the nearest percent, and their total over the array often exceeded 100% per fish. Yet at the outset, independent estimates of the same item did not vary substantially among successive trials, and series tended to regress toward a mean value (an observer's overestimation of volume on one trial was often countered by his underestimation of the same volume on the next). Item volumes were later standardized to 100%. In computing species means, fish with empty guts were not counted and all others were weighted equally, regardless of fish size or gut fullness (cf. Zaret and Rand 1971).

The frequency of occurrence of a dietary item was expressed as the percent of fish with nonempty foreguts that contained the item. The rank order of item frequencies was highly correlated with that of volumes. Kendall's tau correlation coefficients for the kelp perch, white seaperch, and señorita were 0.51, 0.85, and 0.70, respectively ($P<0.01$).

Activity

In the field, feeding bites made by individuals of each species were counted in six, 2-h intervals between dawn and dusk. Standardized as bites per minute, these counts were necessarily limited to solitary individuals that could be followed by a scuba diver for periods of about 3 to 5 min. It was impossible, for example, to discern the very rapid movements of señoritas feeding in large aggregates, which often formed during the early morning hours. The species value for each 2-h interval is the mean of 13-37 observations, each of a different fish. All counts were made during the first week of October, 1974.

To supplement field observations, swimming movements of individuals were observed in an outdoor tank. Fish were caught live either by hook and line during the day or by hand net underwater at night and transported in aerated containers to a 1-m-deep, 500-gallon, circular concrete tank at the University of California Santa Barbara Marine Laboratory. The tank was located outdoors under a lath roof and so was exposed to a natural, but subdued, 24-h cycle of light and dark. To eliminate visual disturbance, a black opaque plastic shroud perforated with several small peep holes was erected around the sides of the tank. Two, 10-W incandescent red lights, placed 1.5 m above the waterline, provided continuous dim light, especially useful for nocturnal observations. The temperature of the continuously running, filtered seawater, which varied no more than 3°C during any 24-h experimental trial, probably approximated that encountered naturally by the species in nearby shallow inshore waters.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

A grid of 10-cm squares was painted on the tank bottom, so that the activity of a fish could be measured as the number of grid lines it crossed during 5-min sample periods, one for each of twelve 2-h intervals (cf. Bortone 1971). On the bottom of the tank were arranged small patches of concrete blocks, rubble, freshly cut kelp, and sand to simulate a natural reef area as much as possible. After each fish had acclimated for a day, it was observed from a platform directly overhead or through the peep holes in the plastic shroud.

Habitat

Habitat occurrences of the three species were determined from previous observations of 414, 2.5-min Super-8 mm underwater movie strips in color (cinetransects) filmed by scuba divers. Cinetransects were made between 1000 and 1500 h during all seasons of 1969-70 and during the fall of 1971 and 1972 in a variety of kelp-bed habitats off the Santa Barbara mainland and Santa Cruz Island (Ebeling, Larson, and Alevizon in prep.). Each cinetransect recorded most fish in a 5-m wide path through or over a particular habitat type and so was classified into scored categories of bottom relief, kelp density, density of low algae on the bottom, and position in the water column ("canopy" or near the bottom). ("Kelp" herein refers to the giant kelp *Macrocystis*; "algae" refers to smaller plants other than giant kelp; and "canopy" refers to the zone of the upper spreading layer of the kelp bed–in our study, within 3 m of the surface.) Fish were tabulated by species as the film was projected in slow motion, reverse, and stop action. Later the frequency of occurrence of each species among all cinetransects was recorded for every habitat parameter.

Concordance, Breadth, and Overlap

For each species, dietary arrays were compared among four "seasons" that correspond roughly to different hydrographic periods off Santa Barbara (cf. Brown 1974): December-February, March-May, June-August, and September-November. Kendall's W coefficient of concordance (Tate and Clelland 1957) was used to measure differences in rank orders of volumes of food items pooled by season. To estimate dietary variability among individuals, concordance was also calculated for each of five or six samples of four to nine fish that were speared at the same general time and place. Thus we assumed that food items must have been about equally available to all the fish in a particular sample.

Breadth and overlap of resource use were computed from values of p_i, the proportion of item i in the sample (fish), or pooled sample of fish (species). For food breadth, p_i is the proportionate volume of any of the species total (S) of different food items; for activity breadth, it is for any of six 2-h daytime intervals, either the proportionate number of bites per minutes by fish in the field or the proportionate number of grid-line crossing per 5-min period by fish in a tank; and for habitat breadth, it is the proportionate occurrence of a species in any of 12 scored categories of habitat: 5 each of kelp density and bottom relief and 2 of depth. Sample values derive only from those resources or activities for which an entire array of items are observable for individual fish, i.e., from food and swimming activity only. Only the habitat parameters that seemed to be mutually independent were included in the analysis. "Density of low algae on the bottom," which was highly correlated with "bottom relief," was excluded. Yet "kelp density" was included. In the study area off Santa Barbara, kelp density is more or less independent of bottom relief because here kelp can anchor to flat as well as high relief bottoms. Because cinetransects were not evenly distributed among habitat categories–most films were taken in relatively dense kelp and high reef–the proportionate frequencies were standardized by total films taken per category.

The sum of p_i^2 over S items in the array equals the probability that any two units selected at random will be of the same item (see Simpson 1949). Thus, the reciprocal, $B = 1/\sum_{i=1}^{S} p_i^2$, measures breadth or diversity (Levins 1968; MacArthur 1972). Or, B is the theoretical number of equally used resources. For example, if all items are in equal proportions, B equals the total items in the array, S. It follows that the value of S determines the maximum value of B. B was computed for fish (individuals within a species) and for pooled sets of fish (individuals pooled by species) as unscaled values and as scaled values. The unscaled values incorporate two contributions to breadth: that of richness (S), and that of evenness of the distribution of amounts among the S items or classes. Values are scaled as B/S between zero, the most uneven distribution possible among S items, and unity, the most even possible.

Proportionate overlap of resource use may be thought of as a measure of mutual use by two species of the same items. The coefficient used here measures overlap between species j and k (Horn 1966):

$$C_\lambda = \frac{2\left(\sum_{i=1}^{S} P_{ij}P_{ik}\right)}{\sum_{i=1}^{S} P_{ij}^{2} + \sum_{i=1}^{S} P_{ik}^{2}}$$

Among the three possible species pairs, activity overlap calculated from field observations of feeding rate varied in the same manner as activity overlap calculated from laboratory observations of swimming rate. For the subsequent calculation of total overlap in food, activity, and habitat, therefore, we used the arithmetic mean of these two independent estimates to express a single activity component.

Two estimates were made of total overlap. If, e.g., food and habitat are mutually independent, i.e., the same foods are available in the same proportions in different habitats, overlap between any species pair is the product of the separate measures for food and habitat. But if food is completely dependent on habitat, i.e., different habitats contain totally different foods, then overlap is the arithmetic mean of the two measures (Pianka 1974). (In the latter case, food and habitat measure the same resource axis, and the separate measures can be thought of as independent estimates of the same overlap.) In general, the actual relation between resource distributions is somewhere between complete independence and dependence. Thus, total overlap as expressed by the mean of the separate overlaps in food, activity, and habitat is a maximum value, and true overlap is somewhere between this and the product estimate (see Pianka 1974).

Kolmogorov-Smirnov tests of goodness-of-fit showed that the distributions of the variates of food breadth (s, b, b/s) differed significantly from normal (were skewed) for the white seaperch and señorita (P = 0.05-0.01), though not for the kelp perch (P>0.05). Therefore, we computed medians, ranges, and the Kruskal-Wallis measure H of differences in location of the ranked variates to test for differences among the three species (see Sokal and Rohlf 1969).

RESULTS

Food

Seasonal Effect

Food arrays were generally correlated among seasons. The rank concordance of diets was significant for all species (Table 1). The same items, which often made up more than 70% of the total food volume, usually occupied one or another of the first three ranks from one season to the next; seldom did the first three positions for any one season contain items not among the first three for the others. Consequently, all samples were pooled by species, regardless of season, for the remaining analyses.

Individual Variability

Food items were generally uncorrelated among fish of the same species collected at the same time and place. Rank concordance was significant for but one of five collections of kelp perch (W = 0.55, P<0.01), and for no collection of white seaperch or señoritas. This might indicate that members of the same species that co-occur were choosing different items from the same forage base. But such a conclusion may be misleading for white seaperch and señoritas. A single item (plant-encrusting bryozoans) usually dominated their foregut contents, and although the second and third ranked items varied considerably among fish, they made up but a minor part of the total.

Kelp Perch

Tiny plankters, mainly copepods, made up more than half of the food consumed by the kelp perch (Table 2). Of 18 categories of items eaten by kelp perch, small calanoid and cyclopoid copepods led in both abundance and frequency; foreguts of six fish contained copepods only, and one was packed with more than 300 individuals. The distinctive genus *Corycaeus* occasionally dominated the contents. Large calanoids longer than 4 mm, which were found in fish collected during late winter only, were relatively rare. Tiny ostracods were frequently consumed, but only in small numbers.

TABLE 1.—Among-season comparison of diets of the three fishes. The first three ranking food items with their percent volume are listed in order for each period. Sample size is the number of diets (fish) pooled per period; W is Kendall's coefficient of rank correlation.

Species	December-February		March-May		June-August		September-November		W
	Item	%	Item	%	Item	%	Item	%	
Kelp perch 18 total items	Sample size = 19		Sample size = 0		Sample size = 12		Sample size = 19		
	Small copepods	50			Gammarid ampnipods	67	Small copepods	42	0.51*
	Plant-encrusting bryozoans	12			Small copepods	14	Gammarid amphipods	26	
	Large copepods	10			Caprellid amphipods	13	Plant-encrusting bryozoans	6	
White seaperch 13 total items	Sample size = 4		Sample size = 24		Sample size = 9		Sample size = 18		
	Plant-encrusting bryozoans	92	Plant-encrusting bryozoans	42	Plant-encrusting bryozoans	45	Plant-encrusting bryozoans	51	0.48*
	Bare plants	5	Bare plants	18	Polychaete worms	25	Crushed shells	28	
	Gammarid amphipods	1.5	Gammarid amphipods	11	Gammarid amphipods	6	Gammarid amphipods	12	
Señorita 19 total items	Sample size = 0		Sample size = 17		Sample size = 17		Sample size = 19		
			Plant-encrusting bryozoans	35	Plant-encrusting bryozoans	65	Plant-encrusting bryozoans	86	
			Gammarid amphipods	11	Serpulid worms	10	Hydroids	5	0.39*
			Hydroids	9	Parasitic copepods	7	Parasitic copepods	3.5	

*Significant at $P < 0.01$

TABLE 2.—Mean proportionate volume and percent frequency of occurrence of 25 food items in foreguts of 50 kelp perch, 55 white seaperch, and 53 señoritas. Food items are listed by their presumed major source.

Food item	Kelp perch		White seaperch		Señorita	
	% vol	% freq.	% vol	% freq.	% vol	% freq.
Primarily planktonic	51.6	—	—	—	7.0	—
Cladocerans	0.5	18.8	—	—	—	—
Ostracods	1.1	20.8	—	—	1.1	13.7
Small copepods (<4 mm)	42.0	81.2	—	—	1.5	15.7
Large copepods (>4 mm)	3.3	18.8	—	—	2.7	11.8
Nauplius larvae	0.2	2.1	—	—	—	—
Zoea larvae	4.3	18.8	—	—	1.7	11.8
Fish eggs	0.2	2.1	—	—	—	—
From process of "cleaning"	2.9	—	—	—	5.4	—
Parasitic copepods	1.4	22.9	—	—	3.5	11.8
Gnathiid isopod larvae	1.4	2.1	—	—	0.2	3.9
Fish scales	0.1	6.2	—	—	1.7	7.8
Primarily substrate oriented: kelp, other algae, and bottom	45.0	—	81.8	—	87.1	—
Free moving	36.2	—	18.1	—	9.7	—
Mysids (kelp)	4.1	18.8	—	—	0.4	7.8
Isopods	0.7	10.4	1.9	9.8	1.3	7.8
Gammarid amphipods	25.7	62.5	8.4	49.0	4.2	27.4
Caprellid amphipods	4.7	12.5	3.3	23.5	2.2	5.9
Decapod shrimps	1.0	8.3	3.2	5.8	0.4	5.9
Unident. crustaceans	—	—	—	—	1.2	5.9
Pycnogonids	—	—	1.3	5.8	—	—
Attached	9.0	—	63.7	—	77.4	—
Bare kelp and other algae	1.5	12.5	0.3	1.9	5.6	15.7
Plant-encrusting bryozoans	7.3	10.4	63.4	63.4	65.5	80.4
Hydroids	0.2	2.1	—	—	5.2	17.6
Serpulid worms	—	—	—	—	1.1	2.0
Primarily substrate oriented: bottom only	—	—	17.7	—	0.2	—
Crushed shells and debris	—	—	12.6	27.4	—	—
Polychaete worms	—	—	3.7	5.8	0.2	2.0
Cumaceans	—	—	0.5	3.9	—	—
Brittle stars	—	—	0.9	1.9	—	—

Small crustaceans that normally move freely on and about the kelp surfaces were almost equal to plankton in dietary importance. Gammarid amphipods, which may cluster just as abundantly about the kelp as in and about the tufted mat of plants and animals on the bottom, ranked second in overall abundance and frequency. Surprisingly unimportant were the so-called "kelp mysids," which are very abundant in the canopy and are commonly eaten by other fishes (Clarke 1971).

Forage on attached organisms was less important. Cheilostomate bryozoans, principally *Membranipora* ("plant-encrusting bryozoans"), ranked a distant third in overall volume. *Membranipora* is the dominant bryozoan encrusting kelp, where it often covers large areas of the plant (Woollacott and North 1971), and most of the bryozoans in the gut contents were associated with bits of kelp blades. Kelp perch apparently ate no benthic prey.

Cleaning activity was but a minor food source. Parasitic copepods, gnathiid isopod larvae, and fish scales were the only items likely to have been ingested in the process. The combined items never contributed more than 5% to the foregut food volume in a single fish.

White Seaperch

Virtually all prey of the white seaperch were substrate oriented, probably picked from off the kelp or bottom (Table 2). Plant-encrusting bryozoans predominated, and when present, averaged 85% of the foregut contents of individual fish. Moving prey, primarily amphipods and shrimps, were much less important. Many of the gammarid amphipods were quite small (<2 mm long); in one fish, e.g., all of 70 individuals did not fill the foregut.

Only the white seaperch ingested appreciable amounts of bottom items. Crushed shells and sand particles, which often were cemented into tubes, ranked second in overall abundance and third in frequency. The remains of polychaete worms were found in but 3 of 14 sand-containing guts, which did, however, include substantial numbers of the gammarids that commonly inhabit such burrows in the tufted mat on the bottom. Relatively large amounts of loose sand in the mid- and hindguts indicated that these fish generally do not winnow non-food items in their mouth.

Señorita

Most of its prey was substrate oriented, probably picked from off the kelp (Table 2). Like white seaperch, señoritas contained a predominance of plant-encrusting bryozoans, but unlike perch, had almost no bottom prey in the foregut. A third of all fish examined contained only the bryozoan *Membranipora* encrusted on pieces of kelp, and bits of bare plant material were found frequently among the encrusted pieces; of a total of 18 categories of food items found in señorita guts, no other so dominated the contents of even a single fish. Hydroids, another item attached to plants and other substrates, ranked third in overall importance. Moving prey, primarily amphipods, were less important.

Unlike kelp perch, señoritas did not exploit plankton as a major source of food. Although some items occurred frequently, they contributed but little to the overall volume.

Cleaning activity did not produce substantial forage, although it contributed relatively more to the diet of señoritas than to that of kelp perch. Of 10 adult señoritas, 142-184 mm long, that contained items likely to have been ingested during cleaning (parasitic copepods, gnathiid isopod larvae, and/or fish scales), the diets of seven were dominated by other food items. Ectoparasites and scales in guts of most señoritas were mixed with other food items, suggesting that the fish had both cleaned and foraged during the same day. However, guts of two of the remaining three fish contained nothing but parasitic copepods and scales. One specimen, collected at 1400 h, contained 465 fish scales, about 90% of the total contents, and 45 parasitic copepods. Both items were distributed more or less evenly throughout the length of the gut, indicating that this fish had cleaned during most of the day.

Diel Forage

All three species fed mostly, if not exclusively, during the day. Foreguts of kelp perch apparently were beginning to fill soon after dawn, were generally full by midmorning, and contained variable amounts of food through dusk (Figure 1). Of 54 day and 38 late-night (midnight-dawn) foreguts examined, 89% and 13%, respectively, contained food. Guts of white seaperch seemed to reach maximum fullness during midmorning and late afternoon. Of 64 day and 22 late-night foreguts examined, 88% and 4%, respectively, contained food. Fullness of mid- and hindguts of both species generally substantiated this daily cycle of feeding (Figure 2). Most foreguts were empty by midnight, when midguts still averaged at least half full and hindguts usually more. Then, by dawn most hindguts were empty, while foreguts were beginning to fill, a general pattern shown by fish whether collected during moonlit or dark nights. Señoritas seemed to feed actively through early afternoon, showing maximum gut fullness about

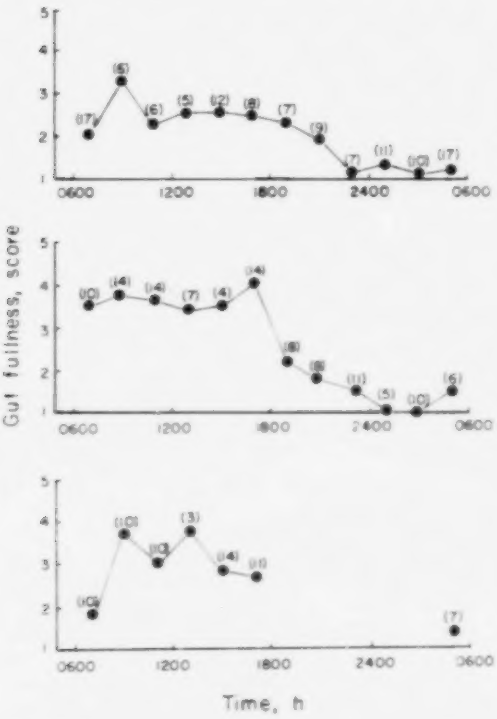

FIGURE 1.—Scored fullness (1, empty – 5, full) of foreguts of: top, kelp perch; middle, white seaperch; and bottom, señorita (which buries itself at night). Each point represents the mean value for (n) individuals collected over a 2-h interval. Time is measured relative to sunrise (0600 h) and sunset (1800 h—see text).

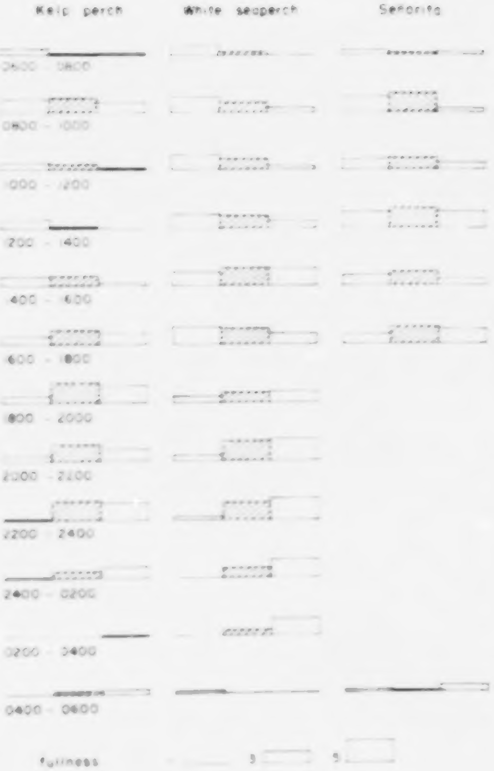

FIGURE 2.—Scored fullness of foreguts (left open bars), midguts (middle hatched bars), and hindguts (right open bars) for the three fishes over 2-h intervals, beginning at dawn. Heights of the bars, scaled at the bottom of the figure, represent mean scores for the numbers of individuals indicated in Figure 1.

midday. Of 65 diurnal foreguts examined, 78% contained food. At night the fish bury themselves in soft areas of bottom (see next section). However, six of seven guts of fish collected at dawn were completely empty.

The duration of passage of food through the guts of the two perches was estimated from their diel feeding cycles. Assuming that feeding stops at dusk when almost half the foreguts were full or nearly so, and that almost all hindguts have emptied by dawn when almost all were, the retention time is probably no more than 10-12 h.

Activity

Feeding Rate

Field observations of feeding bites indicated that kelp perch fed frequently, at a maximum average rate of 20 bites/min around midday, decreasing to zero toward sunset (Figure 3). White seaperch and solitary señoritas fed much more slowly, at maximum rates of only 3.0 and 1.0 bites/min, respectively. Whereas both perches were seen feeding actively throughout the day, señoritas seemed to feed much less intensely after midafternoon. None of the particular individuals followed during the last two daytime intervals were seen to bite. During this time, however, a few other fish were observed picking away at bits of kelp. But this does not modify our general impression that, during the late afternoon hours, most señoritas feed much less actively than earlier in the day.

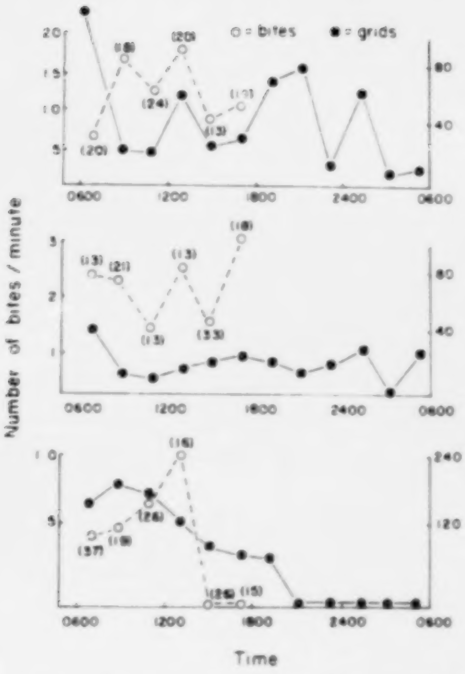

FIGURE 3.–Feeding and swimming activity of: top, kelp perch; middle, white seaperch; and bottom, señorita. Open circles are feeding rates observed in the field and standardized as bites per minute (fish do not feed at night); solid circles are swimming rates observed in a laboratory tank and measured as grid-line crossings per 5-min period. Each point represents the mean value for (*n*) individuals (feeding rates) or five or six individuals (swimming rates) observed for a 2-h interval.

Swimming Rate

Showing little if any spatial or temporal pattern, the two perches swam sporadically throughout the experimental tank during the day and night (Figure 3). Kelp perch swam in spurts and were slightly more active during the day than at night; white seaperch were most active at dawn; and neither species showed any marked change at dusk. The apparent increase in kelp-perch activity at dawn reflected intense swimming by one individual, whose exclusion from the sum would lower the mean species rate to 38 grid-line crossings per 5-min period, about the same as for white seaperch.

In the field during the day, white seaperch swam more continuously in mid-water and near the bottom than did kelp perch, which tended to hover camouflaged among the kelp canopy and only occasionally darted in and out. At night, white seaperch were occasionally seen drifting slowly in mid-water or over the bottom, while kelp perch tended to hang motionlessly among the kelp stipes or even in open water. Kelp perch, especially, were quiescent at night and easily caught with a small hand net then.

Señoritas swam most actively during the morning, then progressively slower throughout the day before finally burying themselves in the sand for the night (Figure 3). Beginning 20 min before sunset during one 24-h trial, a fish that was observed continuously first swam actively throughout the tank, then more restrictively over the sandy area. Finally after swimming in smaller circles about 4-6 cm off the bottom, it turned on its side and, with a few flicks of its caudal fin, proceeded head first into the sand. This entire episode lasted about 10 min, after which the area became dark. Observations by flashlight showed that the fish had buried itself completely, as had three others that accompanied the fish during the trial. Beginning 5 min after sunrise, the four fish emerged within 12 min. Two first stuck their heads above the sand to expose their pectoral fins, then after a short pause, swam out and milled about in small circles. The second pair emerged in a single movement to join the others in a small school, which soon moved throughout the tank. Of the total of seven fish observed in two trials, all buried themselves but one, which lay motionlessly against some bricks and assumed a mottled color pattern.

In the field, three fish observed on separate occasions over a reef about 10 m deep showed settling and burying behavior like that of the experimental animals, although they did not leave to seek a surrounding area of sand flat. Instead, they left a loose aggregation of fish before dusk to remain near the rocky substrate. They gradually restricted their spheres of activity to a small circular area above depressions filled with coarse sand and rubble. Just before sunset when visibility had decreased to about 3 m, the fish became hypersensitive to a diver's light and would dart away quickly when illuminated. About 15 min after sunset, the fish buried themselves in the depressions, first rolling on their sides and then swimming headfirst into the loose substrate. Gentle excavations caused the fish, which were probably buried within the upper 8 cm, to flee quickly. In more than 150 h of scuba diving at night, we have never seen an exposed señorita either over the reef or the surrounding sand flats.

Habitat

Kelp perch were mostly restricted to the canopy, whereas señoritas were more evenly distributed in the water column (Table 3). The kelp perch, whose frequency of occurrence was highly correlated with kelp density, seemed to require the close presence of kelp and was most abundant in the thick of the canopy far above relatively flat bottom areas. Although most frequently filmed in or near the canopy, señoritas ranged throughout the kelp beds and over relatively naked areas of reef. They were recorded from 48% of all cinetransects, as compared to but 26% for kelp perch.

White seaperch were more bottom-oriented than the others, even though they were occasionally seen schooling in mid-water and singly in the canopy. The occurred most frequently in cinetransects taken over areas of sparse kelp and flat bottom at the margins of reefs and kelp beds, but large numbers have also been seen sporadically in areas of highest reef and densest kelp. The cinetransects were limited to areas of reef and kelp and the immediate environs and did not cover the white seaperch's relatively broad range of habitats. Although the kelp perch and señorita are more or less restricted to the habitats covered by the cinetransects, the white seaperch ranges far afield throughout the marginal sandy areas to bays and submerged artifacts, such as piers and docks. Its frequency of occurrence among cinetransects, 10%, was by far the lowest of the three species.

Resource Breadth

Food

Both as a species and as individuals, the kelp **perch had the greatest food breadth** (Table 4, *B*,*b*). The kelp perch ate more items (*S*) than the white seaperch, though amounts were about equally even in distribution (*B*/*S*). The señorita actually ate the most items, but in variable and often small amounts. Although the median number of items in individual foreguts (*s*) was the same for all three species, division between one- and multi-item

TABLE 3.–Distributions of the three fishes among scored categories of four habitat parameters. Parameters of kelp density and density of bottom algae are scored from 1 (absent) to 5 (very dense); bottom relief from 1 (flat) to 5 (high relief rock); and position in water column as C, the canopy within about 2-3 m of the surface, or B, the bottom and immediately overlying waters. Frequency is given as the actual percent (given as whole percent) of total cinetransects scored in the particular category, and as the percent standardized (given as 0.1%) by the total films in each category (see text).

		Kelp density					Bottom relief					Density of bottom algae					Position in water column	
Species	Frequency	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	C	B
Kelp perch	Actual	0	10	15	36	42	52	20	32	4	17	44	27	18	13	14	81	8
	Standardized	0	10.4	14.9	34.3	40.3	40.7	18.2	25.7	3.4	13.4	37.7	23.4	15.4	11.4	12.0	90.8	9.2
White seaperch	Actual	18	9	8	5	11	34	11	7	2	3	22	12	6	1	5	18	1
	Standardized	34.8	17.4	15.9	10.1	21.7	57.0	20.2	12.7	5.1	5.1	45.8	26.4	13.9	2.8	11.1	32.5	67.5
Señorita	Actual	37	48	50	52	34	40	40	53	55	35	33	48	49	32	45	54	45
	Standardized	17.0	21.8	22.6	23.3	15.5	18.2	17.9	23.6	24.3	15.9	15.8	23.2	23.5	15.8	21.9	54.4	45.6
No. of cinetransects per category		16	120	127	125	26	44	59	88	69	131	27	127	148	73	35	154	259

TABLE 4.–Food breadths of the three fishes. The text defines the measure *B* of resource breadth. *S* is the number of food items; *B*/*S* measures the evenness of distribution of proportionate amounts among the *S* items; medians and ranges (in parentheses) describe the individual (fish) variates; and the Kruskal-Wallis *H* statistic, distributed as chi-square with 2 df, tests for differences among species in the sample variates.

		Species (pooled) values			Individual (fish) values		
Species	Sample size	*S*	*B*	*B*/*S*	*s*	*b*	*b*/*s*
Kelp perch	50	18	4.57	0.25	2.0(1-8)	1.70(1.00-3.14)	0.74(0.34-1.00)
White seaperch	55	13	3.39	0.26	2.0(1-5)	1.00(1.00-2.41)	1.00(0.31-1.00)
Señorita	53	19	2.47	0.13	2.0(1-6)	1.22(1.00-4.84)	1.00(0.41-1.00)
				H	12.82*	13.85*	11.81*

*Significant at $P<0.005$

diets was most even in kelp perch. Distributions of all measures (*s*, *b*, *b*/*s*) did not differ significantly from normal for the kelp perch, but were strongly skewed for the others. In fact, median dietary evenness (*b*/*s*) equalled the maximum possible (1.0) for the others, because most foreguts contained either a single item or, occasionally, two items in equal amounts: 55% of the white seaperch and 47% of the señoritas had but a single item, as compared with only 24% of the kelp perch. Moreover, one-item diets of white seaperch and señoritas were more predictable in composition: 73% (of 30 foreguts) and 88% (of 25), respectively, contained the same item, plant-encrusting bryozoans. Other one-item foreguts of seaperch contained either plants (4 foreguts), shrimps (2), or polychaete worms (2). Other one-item foreguts of señoritas had either small copepods (1), gnathiid isopod larvae presumably from cleaning (1), or serpulid worms (1). The 12 one-item kelp-perch foreguts contained either small copepods (6), gammarid amphipods (4), bryozoans (1), or caprellid amphipods (1).

Activity

Activity breadths measured by feeding rates in the field (Table 5, *B*) correspond to breadths measured by swimming rates observed experimentally (Table 6, *B*), even though these two independent measures vary inversely among species. The señorita had the smallest feeding-rate breadth, because bites were observed over the fewest 2-h intervals (Table 5, *S*). From mid-afternoon on, the particular individuals followed during the test were not seen to bite, even though they swam actively about in the kelp canopy and below. (Recall that a few other individuals were feeding, but the general impression was of curtailment of feeding activity then.) Yet the señorita had the largest swimming-rate breadth because it swam actively and continuously during all six daytime intervals (Table 6, *S*). Thus both scaled measures (*B*/*S*) were relatively large for the señorita: the distribution of counts, whether of bites per minute or swimming movements per 5-min period, was relatively even among all intervals in which the action occurred (*S*). But it may be misleading to conclude that señoritas were then most consistent in their daytime feeding activity. During the first four daytime intervals when bites were observed for all species, 40-96% of the kelp perch and 46-69% of the white seaperch were recorded as biting. However, only 13-26% of the señoritas were so recorded. Therefore, señoritas show more variability in feeding activity; i.e., individuals may bite very rapidly for a few minutes then stop for extended periods. On the other hand, individual señoritas were the most consistent in their swimming activity. Señoritas led the others in breadth (*b*) and evenness (*b*/*s*), although the inter-species difference in *b* values was not significant (Table 6).

TABLE 5.–Activity breadths of the three fishes, as measured by their feeding bites per minute in the field. Sample size is the total fish observed in each species; *S* is the number of 2-h intervals (maximum of 6) in which fish were observed to make the biting motions. See Table 4 for further explanation (note that the nature of feeding-bite breadth precludes samples estimates).

Species	Sample size	*S*	*B*	*B*/*S*
Kelp perch	114	6	5.29	0.88
White seaperch	111	6	5.60	0.93
Señorita	139	4	3.62	0.91

Habitat

By all measures, the señorita had the greatest breadth of habitat within the area of reef and kelp where all three species co-occur (Table 7). The kelp perch, which was more or less restricted to the canopy, was most specialized in distribution.

Overlap

The white seaperch and señorita overlapped

TABLE 6.–Activity breadths of the three fishes, as measured by their daytime swimming movements in a large outdoor tank. *S* is the number of 2-h intervals (maximum of 6) in which fish swam across one or more grid lines during a 5-min observation period. See Table 4 for further explanation.

		Species (pooled) values			Individual (fish) values		
Species	Sample size	*S*	*B*	*B*/*S*	*s*	*b*	*b*/*s*
Kelp perch	6	6	4.19	0.70	6.0(2-6)	2.47(1.16-4.83)	0.52(0.29-0.77)
White seaperch	5	6	4.58	0.76	6.0	3.47(2.09-4.85)	0.59(0.35-0.81)
Señorita	6	6	5.53	0.92	5.0(2-6)	4.41(1.95-5.82)	0.96(0.87-1.00)
				H	3.52(NS)	2.39(NS)	11.23*

*Significant at $P < 0.005$

TABLE 7.–Habitat breadths of the three fishes, measured relative to kelp-density, bottom-relief, and position-in-water-column classifications of the cinetransects (see text and Table 2). Sample size is the number of cinetransects from which the species was recorded; S is the number of habitat categories (maximum of 12) in which fish were photographed. See Table 4 for further explanation (note that the nature of habitat breadth precludes sample estimates).

Species	Sample size	S	B	B/S
Kelp perch	109	11	6.32	0.57
White seaperch	42	12	7.61	0.63
Señorita	201	12	9.84	0.82

most in total resource use, with food the main contributor (Table 8). Yet their large food overlap was caused not by any overall similarity in dietary arrays, but by their sharing one predominating item, the plant-encrusting bryozoans. In fact, rank orders of their food items were not significantly correlated (tau = 0.20, P = 0.16).

The kelp perch had the least amount of total overlap with others. Sharing the kelp-canopy area to a great extent, the kelp perch and señorita overlapped most in habitat even though the señorita had the broader overall spatial distribution within the kelp bed. Also, the two species' small food overlap and different activity patterns tended to minimize their total overlap. Actually, rank orders of their food items were significantly correlated (tau = 0.50, P<0.001), because the two species shared similar proportions of a number of minor items. Yet overlap was small because they did not share the same predominating item. A low amount of overlap in total resource use was shown by the two perches. Although their activity patterns were similar, their diets and habitat preferences differed markedly. In diet, they shared neither a predominating food item nor an array of minor items, and rank orders of their items were uncorrelated (tau = 0.06).

DISCUSSION

The kelp perch and señorita–the two species most often involved in cleaning activity–co-occur to a great extent in the sunlit upper waters and eat few if any benthic prey. Kelp perch typically feed in loose aggregations of a few to over 30 individuals. Constantly changing direction and depth, feeding individuals flit about to pick particles from mid-water or, occasionally, from the surfaces of kelp and from other fishes. In calm, clear water, these aggregations often extend to the more open areas between kelp plants. In strong currents, however, the fishes gather in back of kelp columns where the water is quieter and where food swept off the surfaces of kelp may be consumed. Solitary señoritas occasionally nip at various substrates and large drifting particles, but they feed most intensely when in large schools. These schools move in and about kelp stands, momentarily dispersing for individuals to pick and tear at kelp fronds and encrustations, then re-assembling and moving on to another stand of kelp.

The habit of kelp perch and señoritas of cleaning other mid-water fishes probably is incidental to the co-occurrence of the two species in the kelp canopy. Cleaning is not the principal occupation of either species (Limbaugh 1961, Hobson 1971). Their presence in the canopy better relates to their ability to pick small prey from off and from about the kelp blades. Seldom straying far from the heavy foliage where prey may become densely concentrated (Wing and Clendenning 1971), kelp perch also select plankton from incoming currents. Like other diurnal planktivores (Hobson 1974), the kelp perch has a relatively slender body, deeply forked caudal fin, and a slightly upturned mouth (Hobson 1971). Señoritas, which range more widely in the water column from canopy to near bottom, eat much less plankton. They favor attached food, primarily plant-encrusting bryozoans, either from the drift or torn from living plants.

White seaperch, which usually range nearer the bottom and only clean occasionally (Hobson 1971),

TABLE 8.–Overlap in resource use between members of all pairs of the three fishes. Activity overlap is the mean of two independent estimates: from feeding bites observed in the field, and from swimming movements observed in the laboratory. Habitat overlap is measured relative to kelp-density, bottom-relief, and depth classifications of the cinetransects (see Table 3). Total overlap is somewhere between the minimum and maximum estimates.

		Activity				Total overlap	
Overlap between:	Food F	Feeding bites T	Swimming movements M	Activity $A=(T+M)/2$	Habitat H	Minimum FAH	Maximum $(F+A+H)/3$
Kelp perch and white seaperch	0.25	0.92	0.95	0.94	0.63	0.15	0.16
Kelp perch and señorita	0.21	0.85	0.79	0.82	0.79	0.14	0.61
White seaperch and señorita	0.92	0.72	0.76	0.74	0.74	0.50	0.80

show more generalized behavior and are less specialized for picking than either kelp perch or señoritas. Like señoritas, white seaperch ate mostly plant-encrusting bryozoans, but their foraging behavior is quite different. White seaperch typically feed alone or in very small and loose aggregations. Feeding individuals often hover head down within 1 m of the substrate and, judging from their eye movements, search carefully for food. Even so, the substantial amounts of sand and other debris mingled with the more select items in white seaperch guts indicate that once the fish find their sedentary bottom prey, they engulf it in relatively large and indiscriminate mouthfuls.

Underwater disturbances attract white seaperch and señoritas. For example, the two fishes commonly aggregate and feed where bat ray, *Myliobatis californica*, are stirring up the bottom with their wings. They are also quick to follow and assemble about actively working scuba divers. This seems to be an adaptation to forage opportunistically in the wake and disturbance left by others, a strategy which is commonly used by tropical wrasses (Hobson 1974). In contrast, the kelp perch appears to be much less aware of such disturbances and often seems oblivious of an observer at close range.

Indirect evidence suggests that the plant material ingested with the bryozoans is not a primarily source of food for the fish. Only 10% of the ingested material was bare of bryozoans, indicating that white seaperch and señoritas select the heavily encrusted bits. Also, their relative gut lengths are less than expected for herbivores and many omnivores. Odum (1970) noted that the ratio of gut to fish length is usually less than unity in carnivores, one to three in omnivores, and greater than three in herbivores. Mean ratios from 74 white seaperch and 65 señoritas are only 0.82 ± 0.028 (95% confidence interval) and 0.75 ± 0.036, respectively. They do not differ significantly from the mean ratio of 0.76 ± 0.024 from 95 kelp perch, which ingest comparatively little plant material. Likewise, Chao (1973) found no evidence that the cunner, *Tautogolabrus adspersus*, a temperate labrid from off the Atlantic Coast, assimilates the algae it ingests. Small undigested amounts from the intestine of the cunner are usually associated with digested epiphytic animals, including bryozoans. Primarily a shellfish eater, the cunner also has a gut ratio that is less than unity.

Individual diets of kelp perch and señoritas vary considerably from fish to fish, but this is not likely attributable to facultative cleaning. Diets of white seaperch, which do not commonly clean, were no more concordant than those of the other two species. Instead, opportunistic feeding in general may account for most of the variability. Kelp perch may switch from one patch of plankton to another, or feed on the kelp surface as the opportunity arises. Individuals were seen to dart back and forth between open areas and the kelp surface, selecting prey from either source. Although most señoritas eat large amounts of bryozoans, many select small crustaceans, especially amphipods. Hobson (1971) noted that señoritas not only eat mid-water plankton, but are occasionally seen picking about on the bottom. We observed that they are usually among the first to arrive at underwater chumming stations where sea urchins are broken open.

Yet cleaning contributes to the food breadth of kelp perch and señoritas by adding items that can be taken only by that process. And this points out a major problem in measuring food breadth by the "richness" or number-of-items measure, S. The categories of food items cannot be defined objectively, from the fish's point of view at least. For example, the total number of items recorded for the white seaperch would obviously increase if we further diversified the benthic categories (which are not exploited by the cleaners) by—say—distinguishing gastropods from bivalves within the category of "crushed shells." Even though cleaning increases S, its total nutritional importance to the cleaner species may be negligible.

Likewise, it is difficult to conclude whether or not cleaners have specialized diets. The total items eaten by either cleaner exceeded that eaten by the supposedly more generalized white seaperch, and the unscaled food breadth of the kelp perch was greatest of all three species. But the kelp perch and, to a lesser extent, the señorita are in fact limited to smaller items because they have smaller mouths. The 25 subjectively determined food categories included some 15 "small items" (usually <3 mm in diameter) but only 10 "large" (usually >3 mm). Therefore, the diet of the kelp perch appeared to be relatively broad because it includes all of the small items, several of which are exclusively planktonic. On the other hand, the diet of the white seaperch, which rarely visits the canopy, appeared to be more narrow because it includes relatively few of these small prey. Yet having a larger mouth, the white seaperch may eat not only small items, but also an array of items too large to be ingested by the other two.

Other studies indicate that white seaperch forage opportunistically in a relatively broad range of kelp-bed and adjacent habitats. Although plant-encrusting bryozoans were by far their major food in the Santa Barbara areas of kelp and reef, they were of minor importance in fish collected off San Diego. Quast (1968b) reported that 18 fish from a kelp bed contained mostly small crustaceans, worms, and bivalves, while Hobson (1971) noted that 5 fish from shallow areas of surf grass contained small crustaceans, especially caprellid amphipods. DeMartini (1969) concluded that the white seaperch is almost "cosmopolitan" among habitats, including bays and artifacts far from the kelp beds. He observed that, unlike the kelp perch, it has uniformly broad and densely set pharyngeal teeth and commonly eats large, hard-shelled items like barnacles and clams.

Although the kelp perch and señorita have superficially similar feeding mechanisms, they do not overlap broadly in their diets. Off Santa Barbara, in fact, food overlap is least between señorita and kelp perch and greatest between señorita and white seaperch, whose mouth structure and dentition are more generalized. These relations prevail because the kelp perch does not eat substantial amounts of the plant-encrusting bryozoans, the overwhelmingly predominate food item of the other two. Disregarding bryozoans, the remaining (minor) food array of the señorita actually resembles more closely that of the kelp perch than that of the white seaperch. Likewise, off San Diego, kelp perch favor copepods and gammarid amphipods (Quast 1968b), and señoritas favor bryozoans (Quast 1968b; Hobson 1971) but may eat a variety of small crustaceans associated with giant kelp as well (Limbaugh 1955).

Because food overlap between the two cleaners is effectively small, they may co-occur with minimal mutual interference, even though their habitat overlap in the upper kelp bed is relatively broad. Also, their daytime activity patterns differ noticeably. Whereas kelp perch dart sporadically among the kelp blades and seem to feed almost continuously, señoritas move continuously about in open water as well as in dense kelp and seem to feed more sporadically. Also, solitary kelp perch continue their rapid picking about well past mid-afternoon after señoritas were observed to curtail their feeding activity.

It would seem that the señorita and white seaperch are greater potential competitors because they overlap almost completely in both food and habitat within the kelp-bed area. But even so, it is doubtful that availability of their principal food, bryozoans, is a limiting factor in the Santa Barbara area, where encrustations are widespread over the kelp and other substrates. Furthermore, the frequency of occurrence of white seaperch within the kelp bed is quite low compared to that of the señorita. Even though fairly large aggregations are seen occasionally over the reef, the center of abundance of white seaperch may be in more peripheral areas where alternative prey are readily available.

The señorita, which belongs to the large tropical family of wrasses is more specialized in diel behavior than are the kelp perch and white seaperch. Whereas at night the perches simply slow down and become less responsive, the señorita buries itself in pockets of sand or gravel on the reef. Wrasses in general are strickly diurnal: they seek cover and become quiescent at night, as has been observed for tropical species (Hobson 1965, 1968, 1972, 1974; Stark and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972) and for other temperate species (Chao 1973; Olla et al. 1975). Various species hide in holes, bury themselves, and/or protect themselves with mucus envelopes (Hobson 1965, etc.). In the tropics, they are among the first fishes to take cover at dusk and the last to emerge at dawn, a practice that may minimize their vulnerability during the crepuscular hours when predation is most intense (Hobson 1968, 1972; Collette and Talbot 1972). In the kelp beds of the temperate zone, there may be relatively few nocturnal piscivores as compared with the tropics. Thus, the señorita may retain the burying habit of its family (which implies a complex genetic basis) simply because there are no pressures actively selecting against this trait (cf. Hobson 1972).

Many tropical "pickers" have elongated snouts and small mouths with projecting teeth for selecting and removing tiny prey from otherwise inaccessible places (Alexander 1967; Hobson 1968, 1974). These are also adaptations for picking ectoparasites from larger fishes, and indeed many of the small and sharp-nosed tropical-reef fishes are part-time or "facultative" cleaners (Hobson 1971, 1974; Losey 1972). Likewise, the tendency of kelp perch and señoritas to clean may vary among situations or individuals (Hobson 1971) and may provide most fish with only a minor dietary supplement.

CONCLUSIONS

In and about kelp beds off Santa Barbara, the kelp perch, the señorita, and to a lesser extent the white seaperch, belong to a foraging guild of picker-type microcarnivorous fishes. Throughout the year, the kelp perch and señorita, which commonly pick ectoparasites from larger fish, spend most of the day in the sun-lit upper waters in and about the kelp canopy. Here they can discern and pick small prey from various surfaces and from the open water. A more generalized picker, the white seaperch, occurs a bit deeper in the water column and, unlike the two cleaner fishes, eats substantial amounts of benthic prey.

Even though the two co-occurring cleaner fishes have superficially similar feeding mechanisms, they seem to minimize mutual interference in resource use by foraging in somewhat different ways. Thus their total overlap in resource use is relatively small because the kelp perch feeds actively all day and does not eat substantial amounts of plant-encrusting bryozoans, the predominate staple of the señorita and white seaperch.

Within the kelp-bed area, the señorita has the widest habitat breadth. It broadly overlaps the white seaperch's range below the canopy and near the bottom. Their sharing of food and habitat would seem to make these species the greater potential competitors. But even so, they may seldom actually interfere with one another because the white seaperch is not limited to the kelp bed and occurs there less frequently than the señorita.

None of the three species forages at night, when all are relatively inactive and the señorita buries itself in soft substrates on the reef.

Neither the kelp perch nor the señorita obtains substantial amounts of food from cleaning, although some individual señoritas may. Of the two species, the señorita is more specialized in its diel behavior and may be somewhat more nutritionally dependent on cleaning.

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LITERATURE CITED

ALEXANDER, R. M.
1967. Functional design in fishes. Hutchinson and Co., Lond., 160 p.

BORTONE, S. A.
1971. Studies on the biology of the sand perch, *Diplectrum formosum* (Perciformes: serranidae). Fla. Dep. Nat. Resour. Tech. Serv. 65:1-27.

BROWN, D. W.
1974. Hydrography and midwater fishes of three contiguous oceanic areas off Santa Barbara, California. Los Ang. Cty. Mus. Contrib. Sci. 261:1-30.

CHAO, L. N.
1973. Digestive system and feeding habits of the cunner, *Tautogolabrus adspersus*, a stomachless fish. Fish. Bull., U.S. 71:565-586.

CLARKE, W. D.
1971. Mysids of the southern kelp region. *In* W. J. North (editor), The biology of giant kelp beds (Macrocystis) in California, p. 369-380. Nova Hedwigia 32.

COLLETTE, B. B., AND F. H. TALBOT.
1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 98-124. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 14.

DEMARTINI, E. E.
1969. A correlative study of the ecology and comparative feeding mechanism morphology of the Embiotocidae (surf-fishes) as evidence of the family's adaptive radiation into available ecological niches. Wasmann J. Biol. 27:177-247.

EBELING, A. W., W. WERNER, F. A. DEWITT, JR., AND G. M. CAILLIET.
1971. Santa Barbara oil spill: Short-term analysis of macroplankton and fish. U.S. Dep. Commer., Environ. Prot. Agency Off. Water Qual. Proj. 15080 EAL, 68 p.

HOBSON, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.
1971. Cleaning symbiosis among California inshore fishes. Fish. Bull., U.S. 69:491-523.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.

HORN, H. S.
1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419-424.

HUBBS, C. L., AND L. C. HUBBS.
1954. Data on the life history, variation, ecology, and relationships of the kelp perch, *Brachyistius frenatus*, an

embiotocid fish of the Californias. Calif. Fish Game 40:183-198.

Levins, R.

1968. Evolution in changing environments. Princeton Univ. Press, N.J., 120 p.

Limbaugh, C.

1955. Fish life in the kelp beds and the effects of harvesting. Univ. Calif. Inst. Mar. Res., IMR Ref. 55-9, 158 p.

1961. Cleaning symbiosis. Sci. Am. 205(2):42-49.

Losey, G. S., Jr.

1972. The ecological importance of cleaning symbiosis. Copeia 1972:820-833.

MacArthur, R. H.

1972. Geographical ecology: Patterns in the distribution of species. Harper & Row, Publishers, Inc., N.Y., 269 p.

Odum, W. E.

1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*. *In* J. H. Steele (editor), Marine food chains, p. 222-240. Univ. Calif. Press, Berkeley and Los Ang.

Olla, B. L., A. J. Bejda, and A. D. Martin.

1975. Activity, movements, and feeding behavior of the cunner, *Tautogolabrus adspersus*, and comparison of food habits with the young tautog, *Tautoga onitis* off Long Island, New York. Fish. Bull., U.S. 73:895-900.

Pianka, E. R.

1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. U.S.A. 71:2141-2145.

Quast, J. C.

1968a. Fish fauna of the rocky inshore zone. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 35-79. Calif. Dep. Fish Game, Fish Bull. 139.

1968b. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.

Randall, J. E.

1958. A review of the labrid fish genus *Labroides*, with descriptions of two new species and notes on ecology. Pac. Sci. 12:327-347.

Root, R. B.

1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Mongr. 37:317-350.

Simpson, E. H.

1949. Measurement of diversity. Nature (Lond.) 163:688.

Smith, C. L., and J. C. Tyler.

1972. Space resource sharing in a coral reef fish community. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: Ecology of coral reef fishes, p. 125-170. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 14.

Sokal, R. R., and F. J. Rohlf.

1969. Biometry. W. H. Freeman & Company, San Franc., 776 p.

Starck, W. A., II, and W. P. Davis.

1966. Night habits of fishes of Alligator Reef, Florida. Ichthyol. Aquarium J. 38:313-356.

Tate, M. W., and R. C. Clelland.

1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

Wing, B. L., and K. A. Clendenning.

1971. Kelp surfaces and associated invertebrates. *In* W. J. North (editor), The biology of giant kelp beds (Macrocystis) in California, p. 319-339. Nova Hedwigia 32.

Woollacott, R. M., and W. J. North.

1971. Bryozoans of California and Northern Mexico kelp beds. *In* W. J. North (editor), The biology of giant kelp beds (Macrocystis) in California, p. 455-479. Nova Hedwigia 32.

Zaret, T. M., and A. S. Rand.

1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology 52:336-342.

FISHERY REGULATION VIA OPTIMAL CONTROL THEORY[1]

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ABSTRACT

This paper attempts to show how control theory can be used to formulate a regulatory scheme for fisheries. The regulatory mechanism considered is a limit imposed on fishing effort. It is shown that static optimization methods, such as maximum equilibrium yield analysis, need to be supplemented with dynamic methods, such as optimal control theory, which take into account the variable nature of a fishery. The dynamic analysis is used to show that the size of a limit on effort should be a feedback function of the variables in the state of the fishery. The concept of the Linear-Quadratic Optimal Control Problem is introduced as a method for devising such a feedback scheme for fishery regulation.

A single-variable logistic model is used to introduce the basic concepts. A model with three variables is then analyzed to show how the techniques are easily extended to the general multivariable case. Details of the general method are given in an Appendix.

The need for fishery regulation is apparent and will become even more important with the establishment of resource management zones off our coasts. Regulatory mechanisms include catch quotas and limits on fishing effort (number of boats permitted entry into the fishery, number of hooks used, etc.). A mathematical model of the fishery, which includes biological and perhaps economic factors, is useful for determining the best regulatory scheme. Some of the more familiar examples of these models are given by Schaefer (1954, 1968), Beverton and Holt (1957), Ricker (1958), Larkin (1963, 1966), Pella and Tomlinson (1969) and Fox (1970). The above models are said to be dynamic because they utilize differential equations to describe how the fishery changes with time. The inclusion of economic factors, multiple species, and other biological variables, such as size and age, results in multivariable models which are quite complex.

Much of the analysis of fisheries is based on the concept of an equilibrium. Perhaps the best known is the maximum equilibrium yield analysis. However, equilibrium is an idealization and is never actually encountered in reality because continually changing environmental influences act as disturbances which displace the system from its equilibrium condition. For unstable systems this is disastrous because equilibrium is never regained, and for stable systems with large time constants, the return to equilibrium might take so long as to negate the assumptions and usefulness of the equilibrium-based analysis. Thus "static" or equilibrium-based analysis should be supplemented with dynamic methods which take into account the variable nature of the fishery. A purpose of this paper is to show that the above considerations indicate that any regulatory scheme should contain "feedback"; that is, the size of any quota or limit should be a function of the state of the fishery. Also, the concept of the Linear-Quadratic Optimal Control Problem will be introduced as one way of devising such a feedback scheme for fishery regulation.

The Linear-Quadratic Optimal Control Problem, which has been widely applied in engineering, is one method within the larger framework of optimal control theory. Other optimal control methods have recently been applied to problems in fishery management which are unlike the problem treated here. Goh (1969, 1973) applied the so-called "singular" control method to the problem of maximizing yield with a single-species model. Saila (in press) describes Goh's results in more detail. Clark et al. (1973) analyze the problem of optimal reduction of effort in an overexploited fishery. They calculate the fishing mortality function which maximizes the total present value of all profits and utilize a Beverton-Holt model for the fishery. Clark (1973) has presented a similar analysis for a logistic fishery model. The above three analyses lead to control functions which have been loosely described as a "bang-bang" control

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because the optimal values of the control variable lie at its boundaries. Thus the control variable switches between a lower value (usually zero) and an upper value which might be difficult to specify.

There are advantages as well as limitations with the linear-quadratic approach as compared with the bang-bang control approach. With the linear-quadratic approach, quantities such as yield and present value of profits are not directly maximized to obtain the feedback control function, as is done with the bang-bang approach. Rather, the maximization is first done with static methods, and then a feedback control function is constructed to keep the system near the resulting equilibrium condition. To do this, the system equations are linearized about the equilibrium. If disturbances carry the system far from equilibrium, the linearization breaks down. However, this is generally not a serious limitation, since the feedback control function is designed to counteract disturbances and to keep the system near equilibrium. The method is not restricted to equilibrium analysis, and frequently the two approaches are combined by using bang-bang control methods, instead of static methods, to compute an optimal "open-loop" control function. Linearization of the model around the resulting trajectory enables the linear-quadratic method to be used to synthesize a closed-loop (feedback) control function to keep the system on the optimal trajectory (Ho and Bryson 1969).

A significant advantage of the linear-quadratic approach is that it allows the use of linear control theory, whose techniques are more highly developed and easier to apply than the nonlinear techniques required for bang-bang control analysis. Powerful methods of compensating for incomplete information, uncertainties in measurements, model parameters, and model structure are available for the linear-quadratic approach but are scarce for the bang-bang control approach. Also, solutions to bang-bang control problems are extremely difficult to obtain if the model contains more than two variables.

First a single-variable model is used to illustrate the basic concepts. A model with three variables is then analyzed to show how the techniques are easily extended to the general multivariable case. The details of the general method are in the Appendix. There it is also shown in more detail why static optimization methods, such as linear programming, and dynamic optimization methods, such as optimal control theory, should not be treated as competing methods but rather should be used together as part of the total approach to the problem because they are mutually complementary methods. This is mentioned because there is a tendency among economics-oriented analysts to use static methods, whereas analysts with control-theory backgrounds tend toward dynamic methods.

It is assumed that the reader is familiar with the fundamentals of differential equations and matrix operations. A matrix will be denoted by brackets [ ]; a matrix transpose by $[\ ]^T$, and a column vector by a bar underneath, as $\underline{x}$.

SINGLE-VARIABLE MODEL

The following model is the Schaefer or logistic model:

$$\frac{dN}{dt} = aN - bN^2 - qfN. \tag{1}$$

where N is the biomass or number of catchable fish in the fishery, t is time, q is the catchability coefficient, and f is the fishing effort. The constant a is the intrinsic rate of natural increase of the population, and the constant b is related to the carrying capacity of the environment c by the relation: $b = a/c$. The system's equilibrium (N_{eq}, f_{eq}) is found by setting the derivative in Equation (1) equal to zero:

$$0 = aN_{eq} - bN^2_{eq} - qf_{eq}N_{eq}.$$

The equilibrium yield Y_{eq} is:

$$Y_{eq} = qf_{eq}N_{eq} = (a - bN_{eq})N_{eq}.$$

To find the maximum equilibrium yield, we differentiate Y_{eq} with respect to N_{eq}, and set this result equal to zero.

$$\frac{dY_{eq}}{dN_{eq}} = a - 2bN_{eq} = 0.$$

Solving this for the population size and fishing effort corresponding to maximum equilibrium yield, we obtain:

$$N_{eq} = a/2b,$$

$$f_{eq} = \frac{(a - bN_{eq})N_{eq}}{qN_{eq}} = \frac{a}{2q}.$$

Note that a static optimization method, calculus, has been used to find an optimal equilibrium. To analyze the model's behavior in the vicinity of the equilibrium point, Equation (1) is linearized by expanding the right-hand side in a two-variable Taylor series about the point (N_{eq}, f_{eq}), and keeping only the first-order terms (see Appendix). This gives:

$$\frac{dx}{dt} = \left(\frac{\delta g}{\delta N}\right)_{eq} x + \left(\frac{\delta g}{\delta f}\right)_{eq} u$$

where: $g = aN - bN^2 - qfN$

$$x = N - N_{eq} \tag{2}$$

$$u = f - f_{eq}. \tag{3}$$

The new variables x and u are the deviations in population density and fishing effort from their equilibrium values. After evaluating the derivatives of g at the equilibrium point, we obtain:

$$\frac{dx}{dt} = -\frac{a}{2}x - \frac{aq}{2b}u. \tag{4}$$

If the fishing effort is kept constant at its equilibrium value, then $u = 0$ and

$$\frac{dx}{dt} = -\frac{a}{2}x.$$

This system is stable for all positive values of a, which means that if disturbed from equilibrium, the population will eventually return to it. The solution is:

$$x(t) = x(t_o)e^{-\frac{a}{2}(t - t_o)},$$

where $x(t_o)$ is the deviation at time t_o. Since the time constant for this system is $2/a$, it will take that amount of time for the deviation to decay by 63% and for four time constants to decay by 98%. If the constant a is small, this time can be very large. Also, by keeping the fishing effort constant, we cannot take advantage of higher yields obtainable when $x(t_o) > 0$, and risk overexploiting when $x(t_o) < 0$. We will show that by making the fishing effort a function of population level, we can change the system's time constant and also avoid the above difficulties.

For example, the results of Schaefer (1954) give the following values for the Pacific halibut:

$a = 0.67$
$b = 3.05 \times 10^{-9}$
$q = 3.95 \times 10^{-5}$

where N is in pounds, t in years, and f in number of skates. A standard skate of halibut gear consists of eight lines of 300 feet each in length, with shorter lines with hooks attached at 10-foot intervals (Carrothers 1941). The time constant is 3 yr, and thus 12 yr are required for a deviation in population to disappear, assuming no other disturbances act during that time.

If we now specify, by means of a "performance index," that we wish to keep N near N_{eq} while minimizing the variation in f required to do so, we can design a regulatory procedure which will keep the fishery near the maximum equilibrium yield condition. The performance index J which specifies this desire is the so-called quadratic index:

$$J = \int_0^{\infty} (Qx^2 + Ru^2)\, dt.$$

The squared terms indicate that we make no distinction between positive and negative deviations from equilibrium. The positive constants Q and R are the weighting factors which indicate the relative importance placed on keeping N near N_{eq} (x near 0) versus keeping f near f_{eq} (u near 0). The infinite upper limit indicates that we are interested in long-term as well as short-term effects of our fishing effort regulation.

The problem of determining the function u, which minimizes the performance index, is solved by the application of optimal control theory. Since the system, Equation (4), is linear, and the index is quadratic, the problem formulated above is referred to as the Linear-Quadratic Optimal Control Problem.

The solution for the control function is (see Appendix):

$$u = -Kx \tag{5}$$

$$K = -\frac{1}{R}\,\frac{aq}{2b}\,P$$

where P is the positive steady-state solution of the so-called Riccati equation:

$$\frac{dP}{dt} = -aP - \frac{1}{R}\left(\frac{aq}{2b}\right)^2 P^2 + Q$$

with initial condition $P(0) = 0$. The solution for P is:

$$P = \frac{-aR + a\sqrt{R^2 + q^2a^2RQ/b^2}}{q^2a^2/2b^2}$$

Thus P and K are functions of the weighting factors R and Q, which must be specified.

Note that this method yields three results: 1) that the optimal control function for u is a linear function of x (a linear feedback law); 2) the means to calculate the feedback gain K, once R and Q are specified; and 3) that K is negative in this example (we assume that a, b, and q are positive). The third result indicates that the control law, Equation (5), opportunely calls for an increase in fishing effort when the population increases ($x > 0$), and conservatively calls for a decrease in effort when the population decreases ($x < 0$).

In this simple single-variable case we can utilize the first result and avoid specifying R and Q by substituting u from Equation (5) into Equation (4). The result is:

$$\frac{dx}{dt} = \left(\frac{qa}{2b}K - \frac{a}{2}\right)x.$$

The time constant for this system is:

$$\tau = \frac{1}{\dfrac{a}{2} - \dfrac{qa}{2b}K}. \qquad (6)$$

Using this approach it is possible to choose K so as to give a desired value of the time constant.

Alternately, K may be chosen by specifying the magnitude of the deviation in fishing effort we will allow in order to counteract an expected deviation in population level. Written in terms of magnitudes, Equation (5) becomes:

$$K = -\frac{u_m}{x_m}$$

where: x_m = maximum magnitude expected for x
u_m = maximum magnitude specified for u.

Once K has been determined, f as a function of N can be found by substituting x and u from Equations (2) and (3) into Equation (5) to obtain:

$$f = f_{eq} - K(N - N_{eq}). \qquad (7)$$

To evaluate the effects of the above regulation scheme under various conditions, the above expression is substituted into Equation (1), which can then be solved by computer for N and f as functions of time.

As an example with the previously mentioned results of Schaefer (1954) for the Pacific halibut, a maximum deviation in N of 5% from N_{eq} was postulated, and a maximum deviation in f of 5% from f_{eq} was specified. Thus:

$$N_{eq} = a/2b = 1.098 \times 10^8$$
$$f_{eq} = a/2q = 8.48 \times 10^3$$
$$x_m = 0.05N_{eq}$$
$$u_m = 0.05f_{eq}.$$

Using the second method for computing K, we obtain:

$$K = -\frac{0.05f_{eq}}{0.05N_{eq}} = -0.772 \times 10^{-4}.$$

From Equation (6) the new time constant is found to be 1.5 yr, which is one-half the value for the case without feedback control. The fishing effort found from Equation (7) is:

$$f = \frac{a}{2q} + \frac{b}{q}\left(N - \frac{a}{2b}\right) = \frac{b}{q}N = 0.772 \times 10^{-4}N. \qquad (8)$$

In view of the impossibility of continuously and instantly measuring population size and varying fishing effort, f as given by Equation (8) was interpreted as follows. It was assumed that a limit is imposed on fishing effort at the beginning of each year and held constant during that year, and its value f is calculated from Equation (8), with N being the average population over a yearly interval terminating three-tenths of a year before the imposition of the new limit. That is, three-tenths of a year is allowed for collecting and analyzing the population data used to calculate the next year's limit. With this discretized version of f, computer simulation results show that the system time constant is 1.8 yr, which is reasonably close to the 1.5 yr predicted by the continuous model. Thus it is possible to use the analysis based on the continuous model in the realistic situation involving data-collection limitations and limit-imposition constraints.

THREE-VARIABLE EXAMPLE

An advantage of the optimal control method is its ability to accommodate multivariable system models such as multispecies models; models describing economic as well as biological phenomena; and detailed population models incorporating size, age, temperature, food supply, etc. Once a three-variable example is presented, generalization of the technique to models with more than three variables is straightforward. The following model of a single species population was developed by Timin and Collier (1971) and contains three state variables: N, the population density; W, the mean biomass per organism; and E, the food density. The model is given in dimensionless form, and thus the values of the model variables are relative to reference values. The system's dynamics are described by the following equations:

$$\frac{dN}{dt} = (b-d)N - f \tag{9}$$

$$\frac{dE}{dt} = \sigma - qN - \theta E \tag{10}$$

$$\frac{dW}{dt} = gq - (W+c)b - \mu W - \frac{(W_h - W)f}{N} \tag{11}$$

where: t = time measured in a dimensionless unit equal to the time required for the organism to metabolize an amount of food equal to its own dry weight (usually between two and four weeks for commercial fish species)

b, d = birth and death rates per individual

f = fishing rate

g = the ratio of the quantity (energy ingested minus energy not assimilated, minus energy expended to catch, ingest and assimilate the ingested food) to the amount of energy ingested

q = food ingestion rate per individual

c = coefficient of energy loss associated with births

μ = metabolic heat loss coefficient

σ = rate of food supply

θ = proportionality constant for the rate of food leaving the system through decay or flushing

W_h = mean organism biomass of harvested individuals.

Functional forms and parameters given as typical by Timin and Collier are:

$b = 3.8W^2 - 3.8W + 0.95$

$d = 0.19/(2W-1)$

$\sigma = 3$

$q = \dfrac{W^{2/3}E}{1 + 0.1E}$

$\theta = 0.1$

$g = 0.2$

$c = 0.05$

$\mu = W^{-1/3}$

Static optimization can be used to determine the maximum equilibrium yield condition. For $f_{eq} = 0.005$, the equilibrium values are: $N_{eq} = 0.16$, $E_{eq} = 20.3$, $W_{eq} = W_{h_{eq}} = 0.8$. Following the procedures outlined in the Appendix (Equations (A-2) through (A-4)), Equations (9), (10), and (11) were linearized around this equilibrium to obtain:

$$\begin{bmatrix} \dfrac{dx_1}{dt} \\ \dfrac{dx_2}{dt} \\ \dfrac{dx_3}{dt} \end{bmatrix} = \begin{bmatrix} 0.03 & 0 & -0.56 \\ -5.73 & -0.12 & -0.81 \\ 0.14 & 0.02 & -2.02 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix} + \begin{bmatrix} -1 \\ 0 \\ 0 \end{bmatrix} u \tag{12}$$

where: $x_1 = N - N_{eq}$

$x_2 = E - E_{eq}$

$x_3 = W - W_{eq}$

$u = f - f_{eq}$

The following performance index J describes our desire to keep the system near the desired equilibrium (Appendix, Equation (A-6)):

$$J = \int_0^{\infty} (Q_{11}x_1^2 + Q_{22}x_2^2 + Q_{33}x_3^2 + Ru^2)\,dt. \tag{13}$$

Here the weighting matrix $[Q]$ becomes:

$$[Q] = \begin{bmatrix} Q_{11} & 0 & 0 \\ 0 & Q_{22} & 0 \\ 0 & 0 & Q_{33} \end{bmatrix}$$

and the matrix $[R]$ becomes a scalar R. A substantial difference between the single-variable and multivariable cases is that in the latter case we can no longer easily determine the feedback gains by specifying the desired values of the time constants. Instead, the gains are calculated by specifying the components of the weighting matrices. A common procedure for doing this is to choose the components by the rule:

$$Q_{11} = \frac{1}{x_{1m}^2} \qquad R = \frac{1}{u_m^2}$$

where x_{1m} is the maximum desired magnitude of the deviation x_1 of the population N, and u_m is the maximum desired magnitude of the deviation u of the fishing rate f. The components Q_{22} and Q_{33} are chosen in a similar manner. Here we assume the maxima are specified to be:

$$\begin{aligned} x_{1m} &= 5\% \text{ deviation from } N_{eq} = 0.008 \\ x_{3m} &= 1\% \text{ deviation from } W_{eq} = 0.008 \\ u_m &= 50\% \text{ deviation from } f_{eq} = 0.0025. \end{aligned}$$

Thus:

$$\frac{1}{x_{1m}^2} = \frac{1}{x_{3m}^2} = 1.6 \times 10^4 = 0.1\ \frac{1}{u_m^2}.$$

Assuming that the variation x_2 in the food density is not of direct interest, we set $Q_{22} = 0$. Since J from Equation (13) depends only on the relative magnitudes of the weighting factors, we can choose these factors to be:

$$\begin{aligned} R &= 1 \\ Q_{11} = Q_{33} &= 0.1 \\ Q_{22} &= 0. \end{aligned}$$

For this three-variable model, the symmetric Riccati matrix $[P]$ has nine elements, three of which are redundant. Computer solution of the six coupled differential equations resulting from Equation (A-9) and use of Equations (A-7) and (A-8) yield the following feedback control function:

$$u = -[K]x = 0.149x_1 + 0.00027x_2 + 0.026x_3 \quad (14)$$

Use of Equation (14) and the definitions of x_1, x_2, x_3, and u gives the optimal fishing effort as a feedback function of the system variables:

$$\begin{aligned} f = f_{eq} &+ 0.149\,(N - N_{eq}) \\ &+ 0.00027\,(E - E_{eq}) + 0.026\,(W - W_{eq}). \end{aligned}$$

Substitution of the equilibrium values gives:

$$f = -0.045 + 0.149N + 0.00027E + 0.026W. \quad (15)$$

Substitution of u from Equation (14) into Equation (12) gives the set of linearized equations describing the behavior of the model under feedback control. The matrix $[A]$ to be used in Equation (A-5) becomes

$$[A] = \begin{bmatrix} -0.119 & -0.00027 & 0.534 \\ -5.73 & -0.12 & -0.81 \\ 0.14 & 0.02 & -2.02 \end{bmatrix}$$

The roots of Equation (A-5) are: $s = -2.09, -0.096 \pm 0.17j$, where $j = \sqrt{-1}$. The dominant time constant is the negative reciprocal of the least negative real part, and here is equal to $1/0.096 = 10.4$ time units. In a similar way the dominant time constant for the system without feedback is 45.5 time units. Thus the feedback control given by Equation (15) reduces the effects of disturbances in one-fourth the time. These linearized results have been verified by simulation of the original nonlinear model. Other simulations are discussed by Palm (1975).

Before concluding this example, we note from Equation (15) that f is a function of all three variables. This is due to the coupling between the three equations. Also, although the choice of the weighting factors is somewhat arbitrary, this should not obscure the fact that the Linear-Quadratic Optimal Control Problem provides a systematic method for determining the feedback gain matrix $[K]$. A systematic approach is needed because the number of components of $[K]$ becomes so large for multivariable problems that a trial-and-error approach is prohibitive. As long as $[Q]$ and $[R]$ are chosen to be positive-definite, the resulting $[K]$ will stabilize the system. Various choices of $[Q]$ and $[R]$ merely affect the time constants and form of response (oscillatory vs. non-oscillatory return to equilibrium). This is the main advantage of this technique.

With this model the effects of mesh size regulation can be studied by using W_s as an additional control variable. Also, the food supply rate ω is another possible control variable if the model is used to analyze fish farming. The linear-quadratic control technique could be used in both cases.

CONCLUSION

In this introductory paper we have presented only the deterministic case of the Linear-Quadratic Optimal Control Problem. In order to set limits on fishing effort which are functions of system variables such as population density or mean organism weight, it is necessary to measure these variables. Any measurement process is stochastic or noisy, and it is necessary to compensate for this in the design of a feedback regulation scheme. In many engineering applications this has been successfully accomplished by the use of the Kalman-Bucy filter (Athans 1971). In addition, it may be impossible even to measure some variables. This problem of incomplete information has been frequently solved by the use of the Observer Theory (Kwakernaak and Sivan 1972).

Also there will be uncertainties in the determination of the model constants. In fact the "constants" may not be constants at all, but merely the representation of several effects lumped together. Thus there is also error in the model structure, since the model constants are actually variables dependent upon a variety of effects. For the Schaefer model these effects would be interspecies interactions, age structure, availability and vulnerability of the age groups, and physical environment influences on the biological processes. Such difficulties are amenable to solution by adding a "noise" term to the model equations and by modifying the linear-quadratic techniques to accommodate these stochastic effects (Athans 1971). It should also be pointed out that compensation for modeling errors is one of the purposes of feedback control.

The change in model parameters with time can be compensated for by regularly recomputing the feedback gains as more data becomes available. Finally, while no pretense is made of being able to predict exact time paths, the methods described in this paper should prove useful in providing management guidelines. The effects of stochastic processes and uncertainties can be handled in a manageable way by computer simulation, and prediction of the future course of the managed fishery, in an average sense, can be made with appropriate error bands placed on the predictions.

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LITERATURE CITED

ATHANS, M.
1971. The role and use of the stochastic linear-quadratic-gaussian problem in control system design. Inst. Electr. Electron. Eng., Trans. Autom. Control AC-16:529-551.
BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 19, 533 p.
CARROTHERS, W. A.
1941. The British Columbia fisheries. Univ. Toronto Press, Toronto, 136 p.
CLARK, C., G. EDWARDS, AND M. FRIEDLANDER.
1973. Beverton-Holt model of a commercial fishery: Optimal dynamics. J. Fish. Res. Board Can. 30:1629-1640.
CLARK, C. W.
1973. The economics of overexploitation. Science (Wash., D.C.) 181:630-634.
FOX, W. W., JR.
1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80-88.
GOH, B. S.
1969. Optimal control of the fish resource. Malayan Sci. 5:65-70.
1973. Optimal control of renewable resources and populations. (Summary of paper presented at the 6th Hawaii International Conference on System Sciences) 5 p.
HO, Y. C., AND A. E. BRYSON.
1969. Applied optimal control: Optimization, estimation and control. Blaisdell, Waltham, Mass., 481 p.
KWAKERNAAK, H., AND R. SIVAN.
1972. Linear optimal control systems. Wiley - Interscience, N.Y., 575 p.
LARKIN, P. A.
1963. Interspecific competition and exploitation. J. Fish. Res. Board Can. 20:647-678.
1966. Exploitation in a type of predator-prey relationship. J. Fish. Res. Board Can. 23:349-356.
PALM, W. J.
1975. An application of control theory to population dynamics. *In* E. O. Roxin, P. T. Liu, and R. L. Sternberg (editors), Differential games and control theory, p. 59-70. Marcel-Dekker, N.Y.
PELLA, J. J., AND P. K. TOMLINSON.
1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm., Bull. 13:419-496.
RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.
SAILA, S. B.
In press. Some applications of optimal control theory to fisheries management. Trans. Am. Fish. Soc.
SCHAEFER, M. B.
1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-Am. Trop. Tuna Comm., Bull. 1:25-56.
1968. Methods of estimating effects of fishing on fish populations. Trans. Am. Fish. Soc. 97:231-241.
TIMIN, M. E., AND B. D. COLLIER.
1971. A model incorporating energy utilization for the dynamics of single species populations. Theor. Popul. Biol. 2:237-251.

APPENDIX

The Linear-Quadratic Optimal Control Problem and its solution are now outlined. For a thorough discussion, see Ho and Bryson (1969) or Kwakernaak and Sivan (1972). By use of state variable notation, any set of time-invariant ordinary differential equations can be put into the following form:

$$\frac{d\underline{y}}{dt} = \underline{g}(\underline{y}, \underline{f}) \qquad \text{(A-1)}$$

where $\underline{g}$ is a general n-dimensional vector function, $\underline{y}$ is the n-dimensional state vector for the model, and $\underline{f}$ is the m-dimensional input or forcing function vector. If this system has an equilibrium $(\underline{y}_{eq}, \underline{f}_{eq})$, **the following set of algebrais equations must be satisfied:**

$$\underline{0} = \underline{g}(\underline{y}_{eq}, \underline{f}_{eq}).$$

The values of $\underline{y}_{eq}$ and $\underline{f}_{eq}$ depend on the system's parameters, and static optimazation methods such as calculus or linear programming can be applied to find the optimal $\underline{y}_{eq}$, $\underline{f}_{eq}$ and system parameters according to some criterion. This was done in the first example to determine the condition of maximum equilibrium yield. Since any real system is subjected to varying conditions and disturbances, it will be continually displaced from equilibrium. Thus for unstable systems or stable systems with large time constants, a static method of analysis is not sufficient. In such a case the next step is to apply a dynamic optimization method, such as the method presented here, to devise a control scheme which ensures that the system will return to equilibrium with a satisfactory time constant. Thus static and dynamic methods should not be viewed as alternative approaches to optimization, but rather as mutually complementary methods.

After the equilibrium is determined, Equation (A-1) is linearized by expanding the function $\underline{g}$ in a Taylor series in $\underline{y}$ and $\underline{f}$, and keeping only the first-order terms. This gives the linearized model:

$$\frac{d\underline{x}}{dt} = [A]\underline{x} + [B]\underline{u} \qquad \text{(A-2)}$$

where: $\underline{x} = \underline{y} - \underline{y}_{eq}$

$\underline{u} = \underline{f} - \underline{f}_{eq}$

$$[A] = \left[\left(\frac{\partial \underline{g}}{\partial \underline{y}}\right)_{eq}\right] \qquad \text{(A-3)}$$

$$[B] = \left[\left(\frac{\partial \underline{g}}{\partial \underline{f}}\right)_{eq}\right] \qquad \text{(A-4)}$$

in which the subscript eq indicates that the partial derivatives of $\underline{g}$ are evaluated at the equilibrium. The stability of the equilibrium can be determined from the roots of the determinant equation:

$$\left| s[I] - [A] \right| = 0 \qquad \text{(A-5)}$$

where $[I]$ is the $(n \times n)$ identity matrix. The equilibrium is stable if and only if all of the roots s have negative real parts.

By finding the function $\underline{u}$ which minimizes the following quadratic performance index, $\underline{x}$ and $\underline{u}$ are kept near zero and thus the system is kept near equilibrium.

$$J = \int_0^{\infty} (\underline{x}^T [Q] \underline{x} + \underline{u}^T [R] \underline{u})\, dt. \qquad \text{(A-6)}$$

The feedback control function which minimizes J has been shown to be:

$$\underline{u} = -[K]\underline{x}. \qquad \text{(A-7)}$$

The feedback "gain" matrix $[K]$ is calculated from:

$$[K] = [R]^{-1}[B]^T[P] \qquad \text{(A-8)}$$

where the Riccati matrix $[P]$, an $(n \times n)$ symmetric matrix, is the steady-state solution of the Riccati matrix differential equation:

$$\frac{d[P]}{dt} = [Q] + [A]^T[P] + [P][A]$$
$$- [P][B][R]^{-1}[B]^T[P] \qquad \text{(A-9)}$$

with the initial condition:

$$[P(0)] = [0].$$

The matrix $[P]$ is usually found by numerically solving the Riccati equation until all the components of the solution $[P]$ become constant. This will always occur.

DIFFERENTIATION OF FRESHWATER CHARACTERISTICS OF FATTY ACIDS IN MARINE SPECIMENS OF THE ATLANTIC STURGEON, *ACIPENSER OXYRHYNCHUS*

R. G. Ackman, C. A. Eaton, and B. A. Linke[1]

ABSTRACT

Lipids and fatty acids of two marine-caught specimens of the Atlantic sturgeon, *Acipenser oxyrhynchus*, which spawns and also feeds in freshwater, were examined. Specific fat contents, respectively 47.2 and 25.0% in orange-colored dorsal tissue and 8.5% in both livers, were high but not unexpected for sturgeons generally. In each fish a very consistent basic fatty acid composition of depot fats showed that this fat in various parts of the body had a common function. Depot fat from the fatter fish had high iodine values (ca. 190) while in the leaner fish values were lower (ca. 135) and more typical of sturgeons generally. The fatty acid details of depot fats showed some characteristics of marine fats, such as the presence of the unusual ω1 and ω4 polyunsaturated fatty acids, the low figure for linoleic acid and relatively high proportions of long chain polyunsaturated fatty acids, but were more typical of freshwater fats in the virtual absence of eicosenoic and docosenoic acids. Broadly speaking, the fatty acids of the Atlantic sturgeon seem to place it in a special class of fish with fats generally resembling freshwater fish fats in composition, despite its marine origin.

The Atlantic sturgeon, *Acipenser oxyrhynchus* Mitchill, is widely distributed along the Atlantic coast of North America and is to be distinguished from *A. sturio*, the common sea sturgeon of Europe (Scott and Crossman 1973). The Atlantic sturgeon is an anadromous fish, spawning in freshwater,[2] whereas some other sturgeon species, such as the lake sturgeon, *A. fulvescens*, are restricted to freshwater. The most recent and detailed study of sturgeon lipids and fatty acids has been based on an *A. sturio* specimen, apparently of freshwater origin, as it showed a fatty acid pattern which is characteristic of lipids in freshwater fish (Reichwald and Meizies 1973).

The standard reference book on fatty acids states that sturgeon fats are "of the freshwater type" (Hilditch and Williams 1964) although this view was based on a single analysis of a specimen of *A. sturio* caught in the North Sea (Lovern 1932). We wish to report that a study of two saltwater *A. oxyrhynchus* shows that, during its marine period, the Atlantic sturgeon deposits fat with some composition details corresponding to marine fatty acid characteristics. However the fat definitely lacks other details characteristic of fats of higher marine organisms and thus reinforces the published viewpoint based on the common sea sturgeon of the Northeast Atlantic.

MATERIALS AND METHODS

Samples

Two *A. oxyrhynchus* were acquired from fish traps located in an area of the entrance to Halifax Harbour known as Eastern Passage. Both were male, that taken on 12 October 1968 (A) being 150 cm in length and that taken 30 August 1973 (B) being 155 cm. Fish A was frozen whole at -40°C until dissected in March 1969. Fish B was held overnight in an aquarium and dissected immediately after sacrifice. In both cases sections were cut transversely through the middle of the fish. In fish A this was done while frozen and the cut section included liver which was recovered for study, while in fish B the liver was removed separately from the fish. Both fish showed a soft fatty orange layer between the dorsal skin and muscle, of one or more centimeters in thickness, but thinning down the flanks. Parts of this layer penetrated the muscle, especially between myotomes, and streaks of similar colored material appeared in the muscle. A section through fish B was observed to have a

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[2] Sturgeon were once so common that those blocked by the falls in the Hudson river were taken in large quantities and marketed in New York City as "Albany veal." They appear to be returning to their former habitat in large numbers (R. Severo, New York Times, 9 July 1975).

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white layer 2-3 mm in thickness between the epidermis and the soft orange layer.

Lipid from the orange tissue of fish A was extracted by blending with n-hexane in a Waring Blendor. All other lipids were extracted by the method of Bligh and Dyer (1959). For fish A the samples examined, and lipid recoveries, were liver, 8.5%, orange tissue, 47.2%; muscle freed of all visible orange tissue and fat, 2.0%; and whole steak section, 7.2%. Lipid recoveries from fish B samples were liver, 8.5%; orange tissue, 25.0%; muscle freed of all visible orange tissue and fat, 1.2%; and subdermal white layer, 1.3%. Total lipids from the fish A samples were saponified and non-saponifiable materials removed. The recovered fatty acids were converted to methyl esters with boron trifluoride in methanol. White layer and orange tissue samples from fish B were treated similarly, but the muscle and liver lipids were fractionated on a column of divinylbenzene copolymer beads and eluted with benzene. The purity of the various fractions was monitored by thin-layer chromatography on silicic acid. The major fractions, the triglycerides and the polar lipids with the mobility of phospholipids, were transesterified with BF_3-MeOH. Analyses of recovered methyl esters of fatty acids are given in Tables 1 and 2. Further details of these methods, including gas-liquid chromatography of methyl esters on open-tubular polyester columns, will be found elsewhere (Sipos and Ackman 1968; Ackman, Hooper, and Frair 1971; Ackman and Hooper 1973).

RESULTS AND DISCUSSION

The triglycerides in the two marine *A. oxyrhynchus* were distributed throughout the body in the dorsal fatty layer, in the form of muscle infiltration by this fatty layer, and also in the liver. This is most clearly made evident by comparing the iodine values of the different fats isolated from sturgeon B (Table 2). The white subdermal layer, the orange tissue fat, estimated from thin-layer chromatograms to be >95% triglycerides, and the triglycerides isolated from muscle and liver lipids, all have calculated iodine values in the range 132-139. The two phospholipid fractions have much higher iodine values, as expected for this class of lipids (Ackman 1966). In fish A, the orange tissue fat (a clear oil, estimated to be >95% triglycerides from thin-layer chromatograms) had a calculated iodine value of 186 (Table 1). The liver lipid, also estimated to be mostly

TABLE 1.—Fatty acid composition, in weight percent,[1] for lipids recovered from four tissues of Atlantic sturgeon A.

Fatty Acid[2]	Orange tissue	Muscle (no visible fat)	Whole steak section	Liver
14:0	5.13	2.80	3.61	2.82
Iso 15:0	0.35	0.21	0.27	0.21
Anteiso 15:0	0.16	0.11	0.14	0.10
15:0	0.78	0.53	0.90	0.78
Iso 16:0	0.23	0.12	0.19	0.14
16:0	16.21	17.05	16.34	17.38
Iso 17:0	0.29	0.21	[illegible]	0.25
Anteiso 17:0	0.15	0.10	0.12	0.09
17:0	0.48	0.39	0.40	0.33
3,7,11,15-TMHD	0.37	0.44	0.46	0.09
Iso 18:0	0.11	0.08	0.14	0.12
18:0	1.65	2.91	1.83	2.58
Total saturates	25.3	25.2	25.0	25.1
16:1ω9	0.42	0.59	0.44	0.39
16:1ω7	7.45	5.61	6.25	6.45
16:1ω5	0.29	0.26	0.17	0.26
17:1ω8	0.42	0.30	0.38	0.45
18:1ω11+9	15.69	15.22	15.11	18.27
18:1ω7	4.04	4.35	3.93	5.49
18:1ω5	0.47	0.45	0.31	0.38
19:1ω8	0.33	0.39	0.32	0.56
20:1ω11	0.35	0.20	0.41	0.16
20:1ω9	1.23	0.96	1.34	1.19
20:1ω7	0.86	0.84	1.25	0.81
22:1ω13+11	0.15	0.05	0.13	0.08
Total monoenes	31.9	29.4	30.2	34.7
16:2ω6	0.26	0.12	0.26	0.04
16:2ω4	1.42	1.03	1.17	0.78
18:2ω6	0.85	0.77	0.85	0.84
18:2ω4	0.28	0.31	0.29	0.57
20:2ω6	0.24	0.15	0.35	0.26
16:3ω4	1.61	0.93	1.47	0.43
18:3ω6	0.08	0.13	0.10	0.13
18:3ω4	0.40	0.20	0.32	0.30
18:3ω3	0.28	0.26	0.30	0.33
20:3ω6	0.18	0.16	0.28	0.21
20:3ω3	0.10	0.10	0.12	0.12
16:4ω3	0.17	0.19	0.15	0.03
16:4ω1	1.40	0.90	1.25	0.15
18:4ω3	2.78	1.52	2.25	1.28
18:4ω1	0.83	0.54	0.64	0.67
20:4ω6	1.37	1.83	1.53	1.72
20:4ω3	1.94	1.41	1.64	1.97
22:4ω6	0.13	0.19	0.20	0.26
20:5ω3	18.37	19.15	19.40	14.33
21:5ω3 or 2	0.89	0.84	0.92	0.94
22:5ω6	0.38	0.74	0.54	0.42
22:5ω3	2.21	3.19	2.82	3.40
22:6ω3	6.85	10.88	7.91	10.94
Total polyenes	42.8	45.4	44.8	40.2
Calc. iodine value	186	190	194	182

[1] NSA = no significant amount. Average percentages for some minor components were: iso 14:0, 0.07%; 4,8,12-TMTD, 0.03%; 2,6,10,14-TMPD, 0.03%; 19:0, 0.09%; 20:0, 0.04%; 14:1ω7, 0.02%; 15:1ω8, 0.3%; 19:1ω10, 0.07%; 19:1ω6, 0.06%; 20:1ω5, 0.01%; 22:1ω9, 0.04%; 22:1ω7, NSA; 22:1ω9, NSA; 16:2ω7, 0.02%; 18:2ω9, NSA; 20:2ω9, NSA; 16:3ω3, NSA.

[2] 3,7,11,15-TMHD (phytanate) = 3,7,11,15-tetramethylhexadecanoic acid. 4,8,12-TMTD = 4,8,12-trimethyltridecanoic acid. 2,6,10,14-TMPD (pristanate) = 2,6,10,14-tetramethylpentadecanoic acid.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Fatty acid composition, in weight percent,[1] for lipids recovered from four tissues of Atlantic sturgeon B.

Fatty acid[2]	White subdermal layer	Orange tissue	Muscle (no visible fat)		Liver	
			Triglyceride	Polar lipid	Triglyceride	Polar lipid
14:0	3.75	3.81	3.50	0.75	2.42	1.53
Iso 15:0	0.37	0.35	0.31	0.21	0.20	0.14
Anteiso 15:0	0.20	0.26	0.22	0.11	0.09	0.04
15:0	0.71	0.66	0.52	0.43	0.62	0.72
Iso 16:0	0.18	0.20	0.14	ND[3]	0.16	0.11
16:0	15.46	15.24	14.75	22.42	18.32	25.72
7-MHD	0.33	0.25	0.22	0.11	0.19	0.20
2,6,10,14-TMPD	0.22	0.28	0.18	ND	0.16	NSA
Iso 17:0	0.35	0.29	0.28	0.10	0.33	0.24
Anteiso 17:0	0.19	0.25	0.18	0.07	0.20	0.16
17:0	0.27	0.31	0.27	0.27	0.32	0.74
3,7,11,15-TMHD	1.08	1.38	0.55	0.14	0.05	0.27
Iso 18:0 ?	0.14	0.20	0.20	0.08	0.23	0.35
18:0	2.17	1.96	3.14	8.71	2.67	11.77
19:0	0.15	0.13	0.12	0.33	0.07	0.43
20:0	0.18	0.19	0.14	0.09	0.08	0.31
Total saturates	25.9	26.1	25.1	33.9	26.3	43.0
16:1ω9	0.20	0.25	0.21	0.03	0.20	0.61
16:1ω7	6.22	6.08	5.47	1.01	4.50	1.13
17:1ω8	0.75	0.70	0.63	0.31	0.52	0.09
18:1ω9	25.94	25.67	25.75	11.81	31.16	9.03
18:1ω7	4.00	3.91	5.94	3.94	4.46	4.44
18:1ω5	0.43	0.49	0.71	0.21	0.56	0.21
19:1ω10+8	0.54	0.32	0.61	0.10	0.45	0.14
19:1ω6	0.20	0.22	0.48	0.05	0.21	0.07
20:1ω11	1.27	1.29	1.05	0.13	0.31	0.80
20:1ω9	2.78	2.70	2.40	0.55	2.44	2.00
20:1ω7	2.41	2.40	1.72	0.27	1.41	0.89
20:1ω5	0.22	0.23	0.17	0.02	0.13	0.10
22:1ω13+11	0.51	0.46	0.18	0.10	0.14	0.82
22:1ω9	0.26	0.36	0.16	0.01	0.19	0.13
22:1ω7	0.15	0.16	0.05	ND	0.10	0.09
Total monoenes	46.0	45.5	45.7	18.7	46.9	20.8
16:2ω6	0.15	0.21	0.16	ND	0.04	0.18
16:2ω4	0.85	0.85	0.84	0.12	0.52	0.24
18:2ω6	0.84	0.84	0.77	0.22	0.68	0.52
18:2ω4 ?	0.21	0.20	0.26	0.10	0.51	ND
20:2ω9	0.12	0.07	0.15	Trace	0.19	0.03
20:2ω6	0.52	0.58	0.48	0.16	0.35	0.27
20:2ω4	0.25	0.18	0.18	Trace	0.12	ND
NMID (20:2)	0.44	0.48	0.24	0.03	0.10	0.03
NMID (22:2)	0.50	0.52	0.18	0.01	0.20	0.05
16:3ω4	0.65	0.64	0.70	Trace	0.32	ND
18:3ω6	0.26	0.29	0.19	Trace	0.07	Trace
18:3ω4	0.74	0.68	0.52	ND	0.48	ND
18:3ω3	0.48	0.41	0.38	0.11	0.24	0.16
20:3ω6	0.26	0.19	0.12	0.05	0.14	0.06
20:3ω4	0.16	0.30	0.15	ND	0.35	ND
20:3ω3	0.18	0.27	0.13	0.06	0.31	0.08
16:4ω1	0.61	0.60	0.52	0.02	0.08	0.01
18:4ω3	1.29	1.18	1.12	0.07	0.51	0.08
18:4ω1 ?	0.38	0.37	0.47	0.03	0.33	0.01
20:4ω6	1.40	1.28	1.37	4.78	0.84	6.90
20:4ω3	1.42	1.41	1.18	0.26	1.24	0.37
22:4ω6	0.17	0.51	0.20	0.20	0.29	0.32
20:5ω3	8.82	10.21	10.19	18.61	6.95	7.35
21:5ω2 or 3	0.64	0.66	0.67	0.06	0.62	0.05
22:5ω6	0.56	0.44	0.44	0.26	0.96	0.84
22:5ω3	2.44	2.52	2.57	2.02	4.87	2.86
22:6ω3	3.85	3.32	4.40	18.77	5.10	16.46
Total polyenes	28.1	28.4	29.2	47.4	26.8	36.2
Calc. iodine value	139	136	136	201	132	181

[1] NSA = no significant amount. Average percentages for some minor components from subdermal layer, orange tissue, and triglycerides were: 12:0, 0.04%; 13:0, 0.01%; iso 14:0, 0.04%; 4,8,12-TMTD, 0.05%; anteiso 16:0, 0.02%; anteiso 18:0, 0.02%; iso 19:0, 0.06%; anteiso 19:0, 0.02%; 22:0, 0.01%; 14:1ω7, 0.02%; 14:1ω5, 0.01%; 16:1ω11, NSA; 16:1ω5, 0.08%; 17:1ω6, 0.03%; 18:1ω13, NSA; 18:1ω11, trace; 20:1ω15(?), 0.06%; 22:1ω5, NSA; 18:2ω9, 0.06%; 22:2ω6, 0.11%; 16:3ω3, trace in TG; 20:3ω9, 0.03%; 16:4ω3, 0.01%; 22:4ω3, 0.08%.

[2] 7-MHD = 7-methylhexadecanoic acid from 7-methylhexadecenoic acid (Hooper et al. 1973), measured in hydrogenated esters. 2,6,10,14-TMPD (pristanate) = 2,6,10,14-tetramethylpentadecanoic acid. 3,7,11,15-TMHD (phytanate) = 3,7,11,15-tetramethylhexadecanoic acid. NMID = non-methylene-interrupted dienoic acids. 4,8,12-TMTD = 4,8,12-trimethyltridecanoic acid.

[3] ND = not determined.

triglyceride by thin-layer chromatography, had a similar iodine value, as did the lipid from the steak section of high fat content. This high fat content appears to be normal as Fraser et al. (1961) reported 6.2% fat in a steak from this species. Evidently, the fatty acid compositions of triglycerides for fish A would give high iodine values similar to those for phospholipids, for example in the lean muscle extract which would include about half of each type of lipid. The actual iodine value of the triglyceride of sturgeon A is unusually high for marine fish triglycerides (Ackman 1966) but a considerable range of iodine values appears possible for sturgeon depot fats. The "peritoneal cavity" depot fat of the *A. sturio* examined by Lovern (1932) had an iodine value of 126.5, and that of the corresponding liver lipids was 125. A Pacific coast sturgeon (species unknown) had body and liver oils with respective iodine values of 90 and 95 (Bailey et al. 1952), and the iodine values of fats of three types of flesh from the freshwater *A. sturio* of Reichwald and Meizies (1973) were also low. Two *A. baeri* kept in captivity for several years in the Freshwater Fisheries Research Laboratory in Tokyo were slightly different from each other in fatty acid compositions (Table 3) but the fats in each body sample, dorsal flesh and ventral flesh, were respectively quite similar in each fish although they differed in some details from the liver fatty acids (Shimma and Shimma 1968). These authors specifically note the absence of mesentary fat (cf. Lovern 1932), although they found the testes to be unexpectedly high in fat. Oil from American sturgeon of unspecified origin had an iodine value of 125.3 (Bull 1899) and the liver oil from *A. mikadoi* an iodine value of 157.7 (Tsujimoto 1926). Russian data shows Caspian and Atlantic sturgeon fats as having respective iodine values of 122 and 125 (Zaitsev et al. 1969).

In comparative detail, the fatty acid analyses from sturgeon A show little differences between the fat from steak section, orange tissue, lean muscle, and liver (Table 1). However, the high proportions of 22:6ω3 in the lean muscle and in the liver may reflect inclusion of phospholipids which contained relatively high proportions of 22:6ω3 (compare fish B, polar lipids, Table 2). The analysis of particular lipids from fish B is more appropriate for detailed discussion. The fatty acid composition shows that fat from the subdermal white layer, the orange tissue fat, and the muscle triglycerides are all essentially the same fat. Hake skin fats (*Merluccius capensis* and *M. paradoxus*) resemble adjacent dark muscle fat in fatty acid composition (Wessels and Spark 1973). The fatty acid composition of triglycerides in the liver of sturgeon B is also basically similar but has a few fatty acid characteristics shared with the liver phospholipids. Thus the level of 14:0 is lower and the proportion of 16:0 is higher. However 18:0 is not affected in the liver triglyceride, relative to the other triglycerides, so there is no effect on the total of saturated acids. The total for monoethylenic acids in the liver triglycerides is also nearly the same as in the other triglycerides. Although in detail the 16:1 acids are less in parallel to the phospholipid composition, the 18:1 acids are unexpectedly higher, a characteristic confirmed by fish A liver (Table 1). This intermediate status of the liver triglycerides is also apparent in many details and subtotals among the polyunsaturated acids. A singular exception lies in the low proportion of 20:4ω6, which does not seem to extend to any other "ω6" acid. On the other hand, the observation that 20:5ω3 in the liver triglyceride is not intermediate between the other triglycerides and the liver phospholipid is offset by the higher level of the homologous 22:5ω3. In fish A it is possible that 20:4ω6 is also low in liver lipid (of which a large proportion would be triglyceride) but the lower level of 20:5ω3 is less marked in the fatty acid

TABLE 3. Some fatty acid details, in weight percent, for fats from tissues of three sturgeon examined in Japan (from Shimma and Shimma 1968)

Sample		Fat (%)	Percentages of some important fatty acids in fat								Calc iodine value
			14:0	16:0	16:1	18:1	18:2	20:1	20:5	22:6	
A. baeri (A)	dorsal	7	2.5	18.5	7.5	29.8	1.4	3.3	8.0	18.9	171
	ventral	71	2.3	16.6	9.0	31.0	1.4	4.0	6.9	13.8	160
	liver	38	2.6	15.5	7.6	44.1	1.6	3.5	3.8	9.9	130
A. baeri (B)	dorsal	14	3.7	21.6	10.5	33.1	1.3	2.8	6.5	11.4	140
	ventral	76	3.7	19.7	9.7	29.5	1.7	3.5	6.6	13.6	154
	liver	51	1.6	23.7	6.7	54.4	—	1.9	2.7	5.3	95
A. schrenki	liver	41	1.1	18.5	9.8	45.1	7.9	2.2	2.5	1.8	99

composition of the total lipids of the liver. The significance of these observations is obscure but it is probable that the liver is active in de novo biosynthesis of 16:0 and 18:0 acids. If 18:0 is desaturated to 18:1ω9, it could explain the higher level of the latter in the liver triglyceride in terms of a temporary storage function before distribution elsewhere. The same role could result in the liver triglyceride accumulating 22:5ω3 at an intermediate stage between 20:5ω3 and 22:6ω3 for either conversion or catabolism. The two Atlantic sturgeon do not appear to have as much fat in the liver as observed in other species or perhaps in animals from other habitats. Zaitsev et al. (1969) show 8-16% oil in livers of other than Danube sturgeon, and 8-20% in the latter. The liver of an *A. mikadoi* taken at sea near Hokkaido yielded 52% oil by boiling (Tsujimoto 1926) and Shimma and Shimma (1968) report 38 and 51% lipid in livers of two *A. baeri*.

Among the unusual fatty acids observed in the fat of fish B, special mention should be made of the NMID (nonmethylene-interrupted dienes) [20:2] and [22:2] (Ackman and Hooper 1973; Paradis and Ackman 1975). In vertebrate lipids these unusual fatty acids are apparently deposited in parallel with 20:1 and 22:1. The generally lower levels of the latter in the lipids of fish A resulted in the NMID [20:2] and [22:2] being barely detectable (≤0.01%) and they are not included in Table 1. The food of sturgeons on the Nova Scotian shelf is probably basically bottom invertebrates (Scott and Crossman 1973). Many of these organisms are potential sources of these unusual acids (Ackman and Hooper 1973; Watanabe and Ackman 1974; Ackman et al. in press). These acids do not appear to occur significantly in the oils from pelagic fish and it can be assumed that their occurrence in the sturgeon is a food web effect rather than a peculiarity of the species. The absence of 16:1ω11 and 18:1ω13 suggests that indigenous biosynthesis is unlikely.

The levels of isoprenoid acids in triglycerides of fish B, especially 3,7,11,15-tetramethylhexadecanoic acid (phytanic), are unusually high for marine fish oils (Ackman and Hooper 1968), but the exclusion of these acids from the biospecific phospholipids of animals higher than molluscs has been observed previously (Ackman et al. 1970; Ackman and Eaton 1971; Ackman and Hooper 1973; Hooper et al. 1973). The properties of phytanic acid resemble those of 18:0 and a possible unusual low turnover rate for C_{18} acids (see below) could explain the accumulation of phytanic acid. On the other hand, the relatively lower levels of 4,8,12-trimethyltridecanoic acid and 2,6,10,14-tetramethylpentadecanoic acid (pristanic) are not easily reconciled with this explanation. Some gas-liquid chromatographic evidence based on calculation of retention times indicated the presence of the chain extension product of phytanic acid, 5,9,13,17-tetramethyloctadecanoic, and of 6,10,14-trimethylpentadecanoic acid derived from 4,8,12-trimethyltridecanoic acid (Maxwell et al. 1973). However, these components were only present in trace amounts ≥0.01% and identifications are speculative.

The importance of marine algae (the primary source of phytol from which phytanic acid is derived) in the diet of sturgeons is not known (Scott and Crossman 1973). In freshwater, Atlantic sturgeon do eat algae (Leim and Scott 1966). The unusually high levels of 16:2ω4, 16:3ω4, and 16:4ω1, all of which are primarily algal in origin (Ackman et al. 1968), indicate that plants provide a significant proportion of dietary lipids. The tentatively identified higher homologues 18:2ω4, 18:3ω4, and 18:4ω1 behaved as appropriate polyunsaturated fatty acids on nitromethane enrichment (Jangaard 1965) and on thin-layer chromatography on silver nitrate impregnated silicic acid (Morris 1966), and were eliminated (probably converted to 18:0) on hydrogenation. The retention times in gas-liquid chromatography were appropriate to the proposed structure (Ackman et al. 1974). All of these acids may be found in trace amounts in many marine oils, but in both of the sturgeon oils were of much greater importance than usual. As far as we are aware, these acids originate in marine and not freshwater plant lipids. Their exclusion from the polar lipids indicates that they are biochemically functional. It is known that 16:4ω1 does not chain extend to 18:4ω1 in the rat (Klenk 1963) and the reason for the apparent facile chain extensions in sturgeon could be due to a steady intake of the unusual C_{16} acids or their C_{18} homologues from primary plant lipids, or from the fats of marine invertebrates feeding on macrophytes or unicellular algae, or to a general tendency of sturgeons to chain extend C_{16} acids to a stable accumulation of C_{18} acids. The latter possibility, suggested to explain the accumulation of phytanic acid, is part of the larger question of turnover rates for fatty acids in the marine sturgeon and is linked in turn to the freshwater aspects of their lipid biochemistry. It is probable that marine sturgeon, migrating into freshwater to spawn, live off fat reserves (Scott and Crossman 1973).

The subject of freshwater versus marine fatty acid composition for fish oils and fats has been discussed by various authors (Ackman 1967; Farkas 1971; Ikekawa et al. 1972; Reichwald and Meizies 1973), but not always from the same viewpoint. There is, however, clear agreement that in the depot fats of the sturgeon, from either the freshwater or marine milieu, 18:2ω6 (linoleic acid) is a minor (≤1-2%) component and 20:4ω6 (arachidonic acid) is also of limited significance. The low level of 18:2ω6 is probably a "marine" fat characteristic as most freshwater fish have fats with 5% or more of this acid (Ackman 1967; Farkas and Herodek 1967; Mangold 1973; Reichwald and Meizies 1973). In some other animals such as the turtles, freshwater species freely deposit 18:2ω6 and marine forms do not (Ackman, Hooper, and Frair 1971). Unfortunately, many reports on the composition of freshwater fish fats are confused by fatty acid depositions from rearing on artificial diets exceptionally rich in 18:2ω6 and the normal species pattern may be masked by this factor (Albrecht and Breitsprecher 1969). The higher polyunsaturated acids in depot fats of all sturgeons studied to date are dominated by the C_{20} and C_{22} polyunsaturated fatty acids of the "ω3" (linolenic) family, in all analyses. The figures for total C_{20} and C_{22} polyunsaturated acids in Atlantic sturgeon A correspond fairly closely to those for the marine *A. sturio* examined by Lovern (1932). The tissues sampled by various authors are not always clearly comparable. The "pink calf-like" tissue (3.3% fat) of the sturgeon examined by Reichwald and Meizies (1973) occurs dorsally above the abdominal cavity and is also the main caudal tissue, with the "white lard-like" tissue (52.9% fat) interposed in an arrowhead fashion when viewed in longitudinal section (I. Reichwald, pers. commun.). The location of a transverse section could show quite different relative locations for either tissue. From the fat contents, it appears that our "orange" layer corresponds to the "white" layer of an European sturgeon (Reichwald and Meizies 1973) and possibly to the ventral layer of a Japanese sturgeon (Shimma and Shimma 1968), and our "muscle" corresponds to the "pink" tissue of the former. Among differences in fatty acids of interest listed for different animals may be mentioned 20:5ω3 = ½ 22:6ω3 for two animals kept in captivity on a marine fish diet (Shimma and Shimma 1968, see Table 3) and the virtual absence of 20:5ω3 in the fat of the "white" tissue described by Reichwald and Meizies (1973), although in the "pink" tissue 20:5ω3 > 22:6ω3 agrees with our data, as also reported in less comprehensive studies of European sturgeon (Mangold 1973; Meizies and Reichwald 1973). The depot fats of the marine sturgeon we have investigated had 22:6ω3 at about half the level of 20:5ω3, and we interpret the analysis of the marine *A. sturio* by Lovern (1932) to agree with our data. It appears that at some point in the animals' spawning migration the proportions of these two fatty acids could reverse. Interestingly enough, only one out of four freshwater fish oils (from maria or *Lota lota*) examined earlier contained larger proportions of 22:6ω3 than of 20:5ω3 (Ackman 1967).

The spawning period for Canadian Atlantic sturgeon is presumably in early summer. The two male fish examined showed no gonad development and, therefore, if mature presumably they had spawned and returned to the ocean. Oleic acid (Σ18:1) at 44-49% and palmitic acid (16:0) at 21-23% are indicated by Reichwald and Meizies (1973) and other studies (see above) to be the major components of freshwater sturgeon fats. The depot fats of the two marine Atlantic sturgeon we have investigated differ in that both 18:1 totals are 20-30% (magnitude inversely related to iodine value) and 16:0 is about 15%. The original marine *A. sturio* had about 36% 18:1 and 16-19% 16:0, or in other words, the fats examined by Lovern (1932) displayed a composition for these two fatty acids intermediate to two more recent studies.

The very different iodine values for sturgeon A and B are accounted for mainly by the differences in percentages of 20:5ω3, 22:5ω3, and 22:6ω3 in lieu of 18:1 and other monoethylenic acids, as total saturated acids are in the same proportion of fat in both fish and the proportions of most minor unsaturated acids are not important enough to matter. The monoethylenic fatty acids of fish B (total about 45%) probably are more normal as judged by the various low iodine values in the literature for sturgeon fat. The resolving power of open-tubular gas-liquid chromatograph for methyl esters of monoethylenic fatty acids extends our knowledge of the fatty acid biochemistry of the two Atlantic sturgeon in this study. Virtually no 18:1ω11, which could only come from 20:1ω11, was observed. This indicates that the fish were depositing fat and not catabolizing it. On the other hand, the percentage of 20:1ω7 was about the same as that of 20:1ω9 in the body fats of both sturgeon A and B. Therefore, the pathway $16{:}1\omega7 \rightarrow 18{:}1\omega7 \rightarrow 20{:}1\omega7$ appears to be important, suggesting a period of fatty acid biosynthesis rather than of deposition of exogenous fatty acids. Both fish had about the same percentages of 16:1. Fish A had higher proportions of fat in the muscle than Fish B, and $18{:}1\omega7$ was about a quarter of $18{:}1\omega9$ in this fat. In the leaner fish B, $18{:}1\omega7$ was only about one-fifth of $18{:}1\omega9$, suggesting less activity in de novo biosynthesis. It is possible that the diet of fish A was rich in the polyunsaturated fatty acids, the deposition of which was disturbing the typical species-fat composition. Accordingly, fish A may have been more actively engaged in synthesizing monoethylenic fatty acids, via $16{:}0 \rightarrow 16{:}1\omega7 \rightarrow 18{:}1\omega7$, to achieve this composition. Seals, whose depot fat has a higher iodine value than that of most whales, may show the same monoethylenic fatty acid activity (Ackman, Epstein, and Eaton 1971).

Earlier work on oils from four freshwater fish showed 1-3% 20:1 and about 0.3-0.4% 22:1 (Ackman 1967). Marine fish oils, in our experience, usually show 10% or more of 20:1 and 5% or more of 22:1. The absence of large proportions of 20:1 and 22:1 acids in the marine sturgeon depot fat, even in fish B with the less unsaturated fat, is the key reason for our placing the fat of the marine Atlantic sturgeon in a rather special class of marine fat, or more broadly, in the generally freshwater class of fish fats, as recorded by Hilditch and Williams (1964).

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LITERATURE CITED

ACKMAN, R. G.
1966. Empirical relationships between iodine value and polyunsaturated fatty acid content in marine oils and lipids. J. Am. Oil Chem. Soc. 43:385-388.
1967. Characteristics of the fatty acid composition and biochemistry of some fresh-water fish oils and lipids in comparison with marine oils and lipids. Comp. Biochem. Physiol. 22:907-922.

ACKMAN, R. G., AND C. A. EATON.
1971. Investigation of the fatty acid composition of oils and lipids from the sand launce (*Ammodytes americanus*) from Nova Scotia waters. J. Fish. Res. Board Can. 28:601-606.

ACKMAN, R. G., C. A. EATON, J. C. SIPOS, S. N. HOOPER, AND J. D. CASTELL.
1970. Lipids and fatty acids of two species of North Atlantic krill (*Meganyctiphanes norvegica* and *Thysanoessa inermis*) and their role in the aquatic food web. J. Fish. Res. Board Can. 27:513-533.

ACKMAN, R. G., S. EPSTEIN, AND C. A. EATON.
1971. Differences in the fatty acid compositions of blubber fats from Northwestern Atlantic finwhales (*Balaenoptera physalus*) and harp seals (*Pagophilus groenlandica*). Comp. Biochem. Physiol. 40B:683-697.

ACKMAN, R. G., S. EPSTEIN, AND M. KELLEHER.
In press. A comparison of lipids and fatty acids of the ocean quahaug (*Arctica islandica*) from Nova Scotia and New Brunswick. J. Fish. Res. Board Can.

ACKMAN, R. G., AND S. N. HOOPER.
1968. Examination of isoprenoid fatty acids as distinguishing characteristics of specific marine oils with particular reference to whale oils. Comp. Biochem. Physiol. 24:549-565.
1973. Non-methylene-interrupted fatty acids in lipids of shallow-water marine invertebrates: A comparison of two molluscs (*Littorina littorea* and *Lunatia triseriata*) with the sand shrimp (*Crangon septemspinosus*). Comp. Biochem. Physiol. 46B:153-165.

ACKMAN, R. G., S. N. HOOPER, AND W. FRAIR.
1971. Comparison of the fatty acid compositions of depot fats from fresh-water and marine turtles. Comp. Biochem. Physiol. 40B:931-944.

ACKMAN, R. G., J. D. JOSEPH, AND A. MANZER.
1974. Tentative identification of an unusual naturally-occurring polyenoic fatty acid by calculations from precision open-tubular GLC and structural element retention data. Chromatographia 7:107-114.

ACKMAN, R. G., C. S. TOCHER, AND J. McLACHLAN.
1968. Marine phytoplankter fatty acids. J. Fish. Res. Board Can. 25:1603-1620.

ALBRECHT, M. L., AND B. BREITSPRECHER.
1969. Untersuchungen uber die chemische Zusammensetzung von Fischnahrtieren und Fischfuttermitteln. Z. Fischerei N. F. 17:143-163.

BAILEY, B. E., N. M. CARTER, AND L. A. SWAIN (editors).
1952. Marine oils with particular reference to those of Canada. Bull. Fish. Res. Board Can. 89, 413 p.

BLIGH, E. G., AND W. J. DYER.
1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37:911-917.

BULL, H.
1899. Ueber die Bestimmung stark ungesattiger Fettsauren in den Thranen. Chemiker-Zeitung 23:1043-1044.

FARKAS, T.
1971. A possible explanation for the differences in the fatty acid composition of freshwater and marine fishes. Ann. Biol. Tihany 38:143-152.

FARKAS, T., AND S. HERODEK.
1967. Investigations of the fatty acid composition of fishes from Lake Balaton. Ann. Biol. Tihany 34:3-13.

FRASER, D. I., A. MANNAN, AND W. J. DYER.
1961. Proximate composition of Canadian Atlantic fish. III. Sectional differences in the flesh of a species of *Chondrostei*, one of *Chimaerae*, and of some miscellaneous teleosts. J. Fish. Res. Board Can. 18:893-905.

Hilditch, T. P., and P. N. Williams.
1964. The chemical constitution of natural fats. 4th ed. Wiley, N.Y., 745 p.

Hooper, S. N., M. Paradis, and R. G. Ackman.
1973. Distribution of *trans*-6-hexadecenoic acid, 7-methyl-7-hexadecenoic acid and common fatty acids in lipids of the ocean sunfish *Mola mola*. Lipids 8:509-516.

Ikekawa, N., M. Matsui, T. Yoshida, and T. Watanabe.
1972. The composition of triglycerides and cholesteryl esters in some fish oils of salt, brackish and fresh water origins. Bull. Jap. Soc. Sci. Fish. 38:1267-1274.

Jangaard, P. M.
1965. A rapid method for concentrating highly unsaturated fatty acid methyl esters in marine lipids as an aid to their identification by GLC. J. Am. Oil Chem. Soc. 42:845-847.

Klenk, E.
1963. Uber die Bildung von C_{20} und C_{22} Polyensauren aus $\Delta^{4,7,10,13}$-Hexadecate-traensaure bei der Ratte. Hoppe-Seyler's Z. Physiol. Chem. 331:50-55.

Leim, A. H., and W. B. Scott.
1966. Fishes of the Atlantic Coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

Lovern, J. A.
1932. Fat metabolism in fishes. II. The peritoneal, pancreatic and liver fats of the sturgeon (*Acipenser sturio*). Biochem. J. 26:1985-1988.

Mangold, H. K.
1973. "Unsichtbare" Fette und andere Lipide in Susswasserfischen. Wissenschaftliche Veroffentlichungen der Deutschen Gesellschaft fur Ernahrung, Band 24. "Unsichtbare" Fette und Lipoide in Lebensmitteln. (Dr. Dietrich Steinkopff Verlag, Darmstadt 1973.) p. 32-38.

Maxwell, J. R., R. G. Cox, G. Eglinton, C. T. Pillinger, R. G. Ackman, and S. N. Hooper.
1973. Stereochemical studies of acyclic isoprenoid compounds. II. The role of chlorophyll in the derivation of isoprenoid-type acids in a lacustrine sediment. Acta Geochim. Cosmochim. 37:297-313.

Meizies, A., and I. Reichwald.
1973. Die Lipide im Fleisch und im Rogen frischer und geraucherter Fische. Z. Ernahrungswissenschaft 12:248-251.

Morris, L. J.
1966. Separations of lipids by silver ion chromatography. J. Lipid Res. 7:717-732.

Paradis, M., and R. G. Ackman.
1975. Occurrence and chemical structure of nonmethylene-interrupted dienoic fatty acids in the American oyster *Crassostrea virginica*. Lipids 10:1-8.

Reichwald, I., and A. Meizies.
1973. Die Fettsauren der Lipide im Fleisch von Susswasserfischen und Seefischen. Z. Ernahrungswissenschaft 12:86-91.

Scott, W. B., and E. J. Crossman.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 184, 966 p.

Shimma, Y., and H. Shimma.
1968. Fatty acid composition of *Acipenser baeri* cultivated in Tokyo. Bull. Freshwater Fish. Res. Lab. (Tokyo) 18:179-184.

Sipos, J. C., and R. G. Ackman.
1968. Jellyfish (*Cyanea capillata*) lipids: Fatty acid composition. J. Fish. Res. Board Can. 25:1561-1569.

Tsujimoto, M.
1926. Aquatic animal oils. J. Chem. Soc. Jap. Ind. Chem. Sect. 29:71-75.

Watanabe, T., and R. G. Ackman.
1974. Lipids and fatty acids of the American (*Crassostrea virginica*) and European flat (*Ostrea edulis*) oysters from a common habitat, and after one feeding with *Dicrateria inornata* or *Isochrysis galbana*. J. Fish. Res. Board Can. 31:403-409.

Wessels, J. P. H., and A. A. Spark.
1973. The fatty acid composition of the lipids from two species of hake. J. Sci. Food Agric. 24:1359-1370.

Zaitsev, V., I. Kizevetter, L. Lagunov, T. Makarova, L. Minder, and V. Podsevalov.
1969. *In* Fish curing and processing. Mir Publishers, Moscow (translated by A. de Merindol), p. 68, 562.

ZOOPLANKTON ABUNDANCE AND FEEDING HABITS OF FRY OF PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, AND CHUM SALMON, *ONCORHYNCHUS KETA*, IN TRAITORS COVE, ALASKA, WITH SPECULATIONS ON THE CARRYING CAPACITY OF THE AREA

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ABSTRACT

Juvenile pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*, 28 to 56 mm long (fork length) from Traitors River in southeastern Alaska, fed little in freshwater but fed heavily in the estuary, mainly on pelagic zooplankters. Fry did not feed on cloudy moonless nights. The rate of evacuation of pink salmon stomachs ranged from 6 h at 12.8°C to 16 h at 8.5°C. The abundance of zooplankton ranged from 9 to 154 organisms per liter and quantitatively did not change noticeably while fry were in the estuary. In 1964, 1965, and 1966, the estimated numbers of fry in Traitors Cove was 7, 1, and 4 million, respectively. An attempt was made to estimate the carrying capacity of Traitors Cove, using food consumption and evacuation rates in conjunction with estimates of standing crop of zooplankton. It was concluded that 50 to 100 million additional fry from hatcheries would probably exceed the carrying capacity of the estuary.

With the rapidly growing demand for animal protein and the emergence of new hatchery techniques for pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta* (Bams 1972; Bailey and Heard 1973; Bailey and Taylor 1974), we believe that it is timely to speculate on the capacity of estuaries to support more fry. The Japanese, Russians, and Canadians have a number of major pink and chum salmon hatcheries and spawning channels in operation. Japanese hatcheries released over 800 million pink and chum salmon fry in 1973 (source: Japan Fishery Agency). Individual Russian hatcheries are capable of releasing up to 120 million fry annually (Kanid'yev et al. 1970). The Qualicum River in British Columbia, Canada, now produces about 50 million chum salmon fry annually through a combination of flow control in the natural spawning areas and the operation of a spawning channel (Fraser 1972). The problem of evaluating the carrying capacity of estuaries for artificially produced fry is most pertinent. What, for example, would be the impact of 100 million fry on the available food in Traitors Cove?

Recent technological advances in rearing salmon in hatcheries and spawning channels now make it possible to release tens of millions of pink and chum salmon fry into individual estuaries, but lack of knowledge of the food requirements of these two species in nature makes even the immediate results of such releases uncertain. It is conceivable that a spawning channel or hatchery operation could produce such large numbers of fry that their migratory behavior might be altered, or growth and survival might be reduced because of severe competition for a limited food supply. Ivankov and Shershnev (1968) reported that young pink and chum salmon (50 to 80 mm) had fuller stomachs in years of "scarcity" of salmon than in years of "abundance" in the coastal zone of the southern Kuril Islands.

The survival of fry to a large extent depends on their rate of growth and on their ability to escape from predators. Rapid growth requires suitable temperature, an abundance of food, and a rapid transition from endogenous nutrition, based on yolk reserve, to exogenous feeding on small aquatic organisms. In a study of size-selective predation, Parker (1971) demonstrated that predation decreases with increase in size of the prey species.

The study reported in this paper was undertaken in a southeastern Alaska estuary, Traitors Cove (Figure 1), in 1964-66 to gain further insight into the food requirements and feeding habits of pink and chum salmon fry. Questions asked were: How soon in life does feeding begin? How does the diet of the fry compare with the available food organisms? What are the food consumption rates

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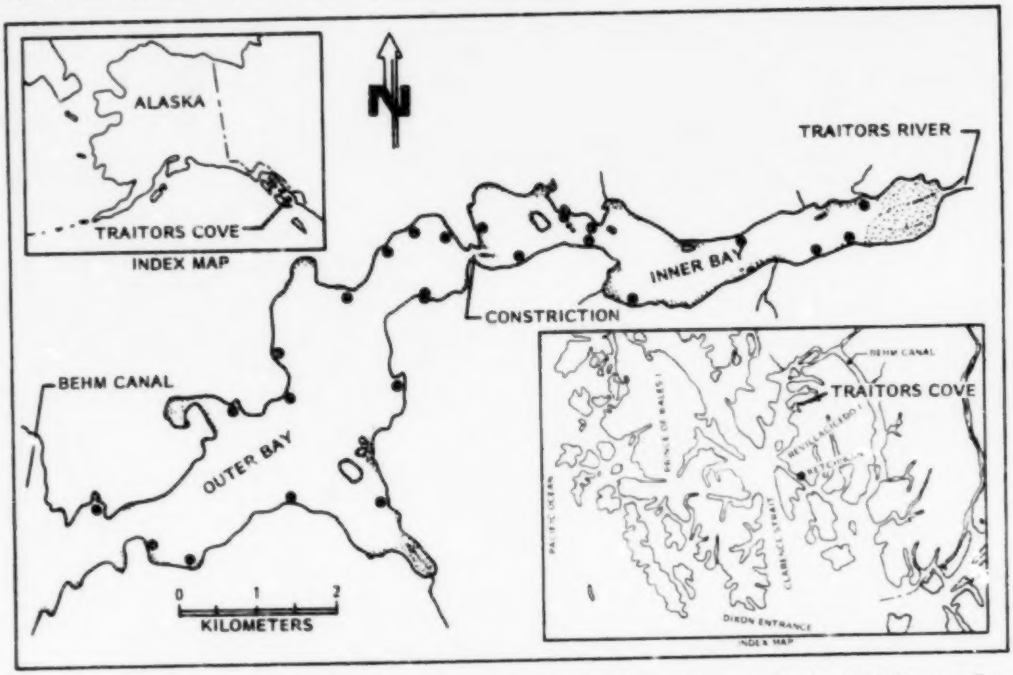

FIGURE 1.—Traitors Cove estuary, Revillagigedo Island, Alaska, 1963-65 (from McLain 1968), showing locations of plankton sampling stations.

for fry in relation to water temperature? How many fry can the estuary support based on estimates of abundance of food organisms and grazing rates?

Traitors Cove is about 50 km north of Ketchikan, Alaska. Several tributaries used by pink and chum salmon enter Traitors Cove, the major one being Traitors River, which has about 55,000 m^2 of spawning grounds. The dominant feature of the estuary is a narrow constriction with a sill, 1 or 2 m below mean low water, which divides the estuary into two basins. The inner bay is about 5.9 km long and 0.7 km wide and has a maximum depth of 46 m. The outer bay is about 6.5 km long and 1.3 km wide and has a maximum depth of 130 m. The tidal range of about 7 m and the constricted flow at the sill create exceptionally strong currents and a reversing tidal falls throughout the year. The turbulence and surface currents affect distribution and movement of fry for at least 0.5 km on both sides of the constriction. We measured surface temperatures of 5° to 13°C in the estuary when fry were present. Some aspects of the oceanography of Traitors Cove have been described by McLain (1968).

Pink and chum salmon fry from the tributary streams enter the estuary from mid-April to late June. Schools with thousands of fry are typically present until late June.

METHODS

To determine if juvenile salmon feed while still in Traitors River, we compared the contents of the entire digestive tracts of individuals excavated from redds with those trapped in nets while migrating downstream at night. All specimens were preserved whole in 10% Formalin solution.[1] The contents of the digestive tract were later removed in the laboratory and examined under a stereoscopic microscope. To determine the kinds and numbers of food organisms eaten in the estuary, we compared stomach contents of fry samples collected in the estuary in 1964, 1965, and

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

1966. Individual food items were measured to the nearest 0.01 mm of body length and diameter with an ocular micrometer to determine volume. Fry in the estuary were collected with a dip net from a skiff and by floating traps anchored near the shoreline. The dip nets and traps were effective in collecting fry less than 60 mm long, which are the subject of this report, but were not effective in collecting larger salmon. The larger fish were able to evade capture by sounding. Most of the fry examined for stomach contents were collected from the estuary during daylight (1100 to 1500). On three occasions, however, fry were collected during nights (0230) when the sky was overcast or moonless and incident light intensity was 0.0 footcandle near the water surface. No stomachs were collected during bright moonlight nights, which were rare.

To estimate the volume of water grazed per day by fry, we measured velocities of water currents close to shore-oriented fry while observing their behavior in relation to the current and food items. Current velocities close to shore-oriented schools of fry were measured by two methods. One method was to record the time it took suspended particles in the water to drift 1 to 5 m along a floating anchored line graduated to 0.1 m. The second method was to measure the velocity by holding a current meter near a school of fish; the meter was attached to the end of a rod about 4 m long. The current meter dial was calibrated to read to the nearest 3 cm/s. Both methods required the observer to operate either from an anchored skiff or from shore. Polaroid glasses were used to reduce glare from the water surface and improve visibility.

Feeding at night by fry was tested in two experiments in an aquarium with known densities of zooplankton. The aquarium consisted of a 7-mil plastic bag suspended in the estuary from a float and containing 76 liters of seawater. The fry were captured in the outer bay and held in a 1-m no. 10 mesh (158-μm openings) plankton net for 20 h to deny them food and to ensure that their stomachs were empty. The starved pink and chum salmon fry together with a known quantity of zooplankton were then placed in the aquarium and held under various light intensities. After timed intervals in the aquarium, fry were removed, killed, and their stomach contents removed.

In the first experiment, fry (length, 32 to 41 mm) in groups of five were placed in an aquarium that contained 240 zooplankters per liter of seawater. A cursory examination of the zooplankters revealed that they were predominantly copepods and barnacle nauplii. Each group of fish was allowed to feed 13 to 28 min before being removed and preserved in 10% Formalin solution. The experiment was started in the evening before sunset and continued until the light meter read 0.0 footcandle. In the second experiment, 14 fry were placed in an aquarium containing about 260 zooplankters per liter; they were kept there for 4 h and 20 min at night before they were removed and preserved in Formalin. The light meter read 0.0 footcandle throughout the experiment.

The time required for fry to evacuate their stomach contents was determined experimentally at 8.5°, 10.0°, and 12.8°C. The procedure was to capture 200 to 300 salmon fry in the estuary and place them in strained seawater in a floating cage of no. 10 mesh plankton net, which prevented entry of prey from the surrounding water. At the start of each test, 10 pink and 5 chum salmon were killed and preserved; at hourly intervals thereafter 5 fish of each species were killed and their stomach contents examined until all 10 fish of two successive samples contained no food in their stomachs. The pink salmon fry examined in these tests ranged from 32 to 57 mm in length and the chum salmon from 34 to 54 mm. Water temperatures were recorded by a thermograph to the nearest 1°C. The sensing probe of the thermograph was located 1 m below the water surface.

The zooplankton in Traitors Cove was sampled only in 1965 and 1966 while fry were in the bay. A 5-inch Clarke-Bumpus sampler with a no. 10 mesh net was towed at a depth of about 0.5 m until about 50 liters of water (2 to 10 s) had been strained. Seventy-nine samples were collected—in 1965, 7 stations in the outer bay were each sampled in 1 day; and in 1966, 10 stations in the inner bay and 14 in the outer bay were each sampled on 3 different days (Figure 1). Only one sample was taken at each station. The zooplankton catch was preserved in 5% buffered Formalin solution. The plankton samples were subsampled by two methods for analysis. In the first method, each of the 79 samples was analyzed from 1-ml subsamples (approximately 1/100 of the sample) placed in a Sedgewick-Rafter chamber. The kinds, numbers, and size of the various plankters were determined. Volumes of the different plankters were computed from lengths and average diameters, assuming a cylindrical shape for each plankter. In the second method, all 7 of the 1965 samples and 66 of the 1966 samples were examined to determine numbers of plankters from larger subsamples ([illegible] of the sample) taken with a Cushing subsampler (Cushing 1961). A comparison of the results of the two analyses indicated that the data from 1-ml subsamples overestimated the number of organisms by an average of 20% (range 15 to 30%). Therefore, estimates of zooplankton densities using the first method were reduced by 20%. Plankton samples contained protozoans (mostly tintinnids) and phytoplankton, but these were not included in the estimate of standing stock of plankton because salmon fry consumed only the larger zooplankters. Rotifers and copepod nauplii were the smallest plankters included in the counts.

FEEDING IN TRAITORS RIVER

Although most of the pink and chum salmon excavated from redds in Traitors River contained items such as sand or detritus in their digestive tracts, only a few individuals contained food organisms. Chironomids (dipterans) were the most frequently observed food item. Seventy juvenile pink salmon (fork length, 33 to 41 mm) were collected from spawning gravels for analysis of contents; only three contained food—a chironomid pupa and some unidentifiable insect remains (Table 1). Seventy juvenile chum salmon (fork length, 33 to 41 mm) were collected from spawning gravels; nine contained food. Chum salmon had eaten only chironomid larvae and pupae, plecopteran nymphs, ephemeropteran nymphs, and an arachnid (spider). One chum salmon (41 mm) contained the remains of 24 chironomid pupae, 2 chironomid larvae, 3 ephemeropteran nymphs, and 3 plecopteran nymphs. The other eight chum salmon that contained food were 37 to 39 mm long and had eaten only one to three items each.

TABLE 1.—Frequency of occurrence of items in digestive tracts of 70 pink and 70 chum salmon juveniles excavated from redds in Traitors River in 1964-65.

Item	Pink salmon		Chum salmon	
	Number	Percent	Number	Percent
Arachnids	0	0	2	3
Ephemeropterans	0	0	2	3
Plecopterans	0	0	2	3
Dipterans	1	1	4	6
Insect remains	2	3	3	4
Plant detritus	15	21	18	26
Fine sand	33	47	44	63
Empty	22	31	12	17

TABLE 2.—Frequency of occurrence of items in digestive tracts of 40 pink salmon fry and 40 chum salmon fry trapped in nets while migrating down Traitors River, May 1964.

Item	Pink salmon		Chum salmon	
	Number	Percent	Number	Percent
Plecopterans	0	0	2	5
Dipterans	0	0	9	22
Insect remains	0	0	2	5
Detritus	1	2	1	2
Fine sand	8	20	22	55
Empty	31	78	19	48

Although none of the 40 downstream-migrating pink salmon fry (length, 32 to 37 mm) contained food, 9 of the 40 chum salmon (length, 35 to 42 mm) contained substantial numbers of chironomid pupae and plecopteran nymphs (Table 2). The average for those that contained food was 6.7 food items (range 1 to 27 items).

Fine sand (diameter, 0.05 to 0.50 mm) and plant detritus were common items in the digestive tracts of both the gravel-resident and the migrating pink and chum salmon (Tables 1, 2). The sand and detritus were more common in fish taken from the redds than in those captured in the downstream traps.

FEEDING IN THE ESTUARY

We studied four aspects of the feeding of pink and chum salmon fry in the estuary: 1) stomach contents, 2) feeding behavior in relation to water currents, 3) effect of daylight on feeding, and 4) time required for evacuation of stomach contents.

Stomach Contents of Pink Salmon Fry

In the springs of 1964, 1965, and 1966, a total of 140 pink salmon (length, 28 to 56 mm) were collected from the estuary during daylight, and 30 (length, 31 to 58 mm) were collected at night (Table 3). All of the stomachs from the fry collected in daylight contained food. Copepods (calanoids and cyclopoids) occurred in 94% of the stomachs and constituted 77% of the total volume of stomach contents. Barnacle nauplii (cirripedes) and cladocerans (*Podon* sp. and *Evadne* sp.) each occurred in 56% of the stomachs and constituted 6% of the total volume. The remaining 11% of the food volume consisted of various other planktonic forms and occasional epibenthic organisms. Most of the food items were between 0.3 and 3.0 mm long. The smallest item in pink salmon stomachs was a disc-shaped diatom and the largest were fish

TABLE 3.—Zooplankton and other organisms from stomachs of 180 pink salmon fry (length, 29 to 36 mm) collected in daylight and 30 (length, 31 to 36 mm) collected at night in Traitors Cove, 1964-66, and percentage relative importance by volume.

Item	Collected in daylight: Percentage stomachs containing item	Collected in daylight: Mean items per stomach: Number	Collected in daylight: Mean items per stomach: Percent	Collected in daylight: Percentage relative importance by volume	Collected at night: Percentage stomachs containing item	Collected at night: Mean items per stomach: Number	Collected at night: Mean items per stomach: Percent	Collected at night: Percentage relative importance by volume
Diatoms	32	2.3	3	+	38	0.4	2	+
Rotifers	15	4.0	3	+	0	0.0	0	0
Bryozoans (cyphonautes)	2	0.0	0	+	0	0.0	0	0
Gastropods (veligers)	12	0.5	0	+	3	0.1	1	+
Pelecypods (veligers)	28	0.8	1	+	0	0.1	1	+
Polychaetes (larvae)	31	1.1	1	1	0	0.3	2	1
Arachnids	2	0.0	0	+	3	0.0	0	+
Cladocerans	56	10.3	8	6	9	0.7	4	3
Copepods	94	78.7	58	77	76	10.7	67	86
Cirripedes (nauplii)	56	18.6	14	6	30	2.1	13	5
Cirripedes (cyprids)	25	1.9	1	2	0	0.4	2	3
Cirripedes (casts)	2	0.1	0	+	0	0.1	1	+
Mysids	4	0.1	0	+	0	0.0	0	0
Cumaceans	3	0.1	0	+	0	0.0	0	0
Isopods	1	0.0	0	+	0	0.0	0	0
Amphipods	4	0.0	0	+	0	0.0	0	0
Euphausiids (larvae)	2	0.1	0	1	0	0.0	0	0
Decapods (zoeae)	9	0.3	0	1	0	0.0	0	0
Unidentified crustaceans (nauplii)	20	1.4	1	+	0	0.1	1	+
Dipterans (larvae)	3	0.0	0	+	3	0.0	0	+
Dipterans (pupae)	6	0.1	0	+	3	0.0	0	+
Larvaceans	26	1.8	1	3	8	0.2	1	2
Eggs (invertebrates)	49	20.8	15	3	23	0.8	5	1
Fish	4	0.0	0	+	0	0.0	0	0

+ indicates less than 0.5%.

larvae (up to 8 mm long). Unidentifiable material occurred in only 11% of the stomachs and constituted an insignificant fraction of the volume.

The 30 pink salmon fry collected from the estuary at night all had food in their stomachs, but they probably had not feed recently. Many more food items were found in the stomachs of pink salmon fry collected in daytime than in those collected at night—an average of 136 items versus 16. Also, digestion had not progressed as far in the daytime fry—only 11% of their stomachs contained unidentifiable items, whereas 80% of the stomachs from nighttime fry contained unidentifiable items. On three moonlight nights, fry were seen dimpling the water surface while apparently feeding. Incident light intensity at the water surface at such times was 0.016 to 1.0 footcandle.

Stomach Contents of Chum Salmon Fry

In the springs of 1964, 1965, and 1966, a total of 124 chum salmon (length, 32 to 51 mm) were collected from the estuary during daylight and 20 (length, 35 to 43 mm) were collected at night (Table 4). All of the fry taken during daylight contained food. Copepods occurred in 73% of the stomachs and constituted 30% of the total food volume. Larvaceans occurred in 54% of the stomachs and constituted 34% of the total food volume. Dipteran (chironomid) pupae occurred in 51% of the stomachs and constituted 11% of the volume. The remaining 25% of the food volume was primarily other planktonic forms (including cladocerans and eggs) but also a few epibenthic animals. Unidentifiable material occurred in 20% of the chum salmon stomachs but constituted an insignificant fraction of the volume and was not included in the final comparisons. Food items eaten by chum salmon fry were similar in size to those eaten by pink salmon, mostly from 0.3 to 3.0 mm long. The largest item was a larval fish 20 mm long. Chum salmon fry, however, tended to feed on larger (Table 5) and harder shelled items than pink salmon, as evidenced by the greater incidence of harpacticoid copepods, collembolans (intertidal springtails), cumaceans, and chironomids in the chum salmon (Tables 3, 4). The chum salmon fry could have picked up some of the so-called epibenthic or intertidal organisms in the form of neuston, or drift material.

Many more food items were found in the stomachs of the chum salmon collected in daytime than in those collected at night—an average of 124 items versus 4. Only 20% of the stomachs collected in daytime contained unidentifiable items versus 70% at night.

TABLE 4.—Zooplankters and other organisms from stomachs of 120 chum salmon fry (length, 32 to 41 mm) collected in daylight and 29 (length, 35 to 43 mm) collected at night in Traitors Cove, 1964-66, and percentage relative importance by volume.

Item	Collected in daylight				Collected at night			
	Percentage stomachs containing item	Mean items per stomach		Percentage relative importance by volume	Percentage stomachs containing item	Mean items per stomach		Percentage relative importance by volume
		Number	Percent			Number	Percent	
Diatoms	16	0.4	1	+	4	0.2	5	+
Rotifers	7	0.5	1	+	0	0.0	0	0
Gastropoda (veligers)	3	0.2	0	+	0	0.0	0	0
Pelecypoda (veligers)	14	0.4	1	+	0	0.0	0	0
Polychaetes (larvae)	21	1.3	2	2	4	0.3	7	1
Arachnida	9	0.1	0	2	0	0.0	0	0
Cladocerans	58	12.9	18	8	0	0.0	0	0
Ostracoda	1	0.0	0	+	0	0.0	0	0
Copepods	73	18.3	27	30	39	1.7	41	37
Cirripedes (nauplii)	34	2.3	3	1	29	0.5	12	6
Cirripedes (cyprids)	20	0.6	1	1	14	0.1	2	1
Cirripedes (casts)	1	0.0	0	+	0	0.0	0	0
Cumaceans	6	0.1	0	1	0	0.0	0	0
Isopoda	2	0.0	0	+	0	0.0	0	0
Amphipoda	3	0.0	0	+	0	0.0	0	0
Euphausiids	1	0.0	0	+	0	0.0	0	0
Decapoda (zoeae)	21	0.4	1	3	0	0.0	0	0
Unidentified crustaceans (nauplii)	10	0.8	1	+	4	0.0	0	+
Collembolans	18	0.4	1	1	0	0.0	0	0
Dipterans (larvae)	10	0.2	0	+	6	0.1	2	2
Dipterans (pupae)	51	3.4	5	11	56	1.3	31	50
Dipterans (adults)	4	0.1	0	+	0	0.0	0	0
Unidentified insect remains	6	0.1	0	+	0	0.0	0	0
Larvaceans	54	19.2	25	24	0	0.0	0	0
Eggs (invertebrate)	19	14.8	9	4	4	0.0	0	+
Fish	6	0.1	0	3	0	0.0	0	0

[1] + indicates less than 0.5%.

Feeding Behavior in Relation to Water Currents

Our visual observations of individual chum and pink salmon fry in shore-oriented schools indicated that their feeding varied with the speed of the water currents. At velocities of 0 to 10.7 cm/s, a fry would typically swim a darting course as much as three times its body length to capture a food item. At higher velocities, 10.8 to 19.8 cm/s, schools of fry sometimes held position relative to the shore or bottom while facing the current, and an individual would typically deviate up, down, or to the sides no more than one-third of its body length to capture oncoming food. At still higher velocities, 19.9 to 24.4 cm/s, fry in schools often held a constant position relative to shore or bottom but did not feed. Fry that appeared to be in visual contact with the shore or bottom avoided currents above 24.4 cm/s unless frightened.

Effect of Daylight on Feeding

The cessation of feeding at night by pink salmon fry was confirmed by the two feeding experiments we conducted in the aquarium. In the first experiment, feeding rate was directly related to light intensity. During a 78-min period when light intensity ranged from 65 to 170 footcandles (three tests), the average consumption was 2.2 to 3.1 zooplankters per minute per fry (Figure 2). At light intensities of 2 footcandles or less, the average feeding rate was only 0.5 zooplankter per minute per fry (three tests). In the second experiment, performed entirely in darkness, little feeding took place. One fry had eaten 48 plankters (less than 0.2 plankter per minute), and the remaining 13 had eaten 13 plankters (0 to 0.001 plankter per minute). These observations agree with laboratory experiments of Hoar (1942) in which young salmon fed little during darkness.

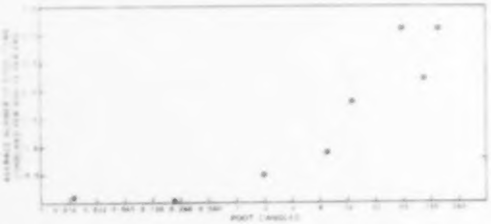

FIGURE 2.—Effect of darkness on feeding rate of pink salmon fry confined in an aquarium. Each dot represents a single test of feeding rate.

TABLE 5.—Average size of zooplankters and other organisms collected by Clarke-Bumpus sampler and present in the stomachs of pink and chum salmon fry at Traitors Cove, 1965-66.

Item and place collected	Number measured	Length (mm)		Diameter (mm)		Average volume (mm³)
		Average	Range	Average	Range	
Diatoms:						
Clarke-Bumpus sampler	24	0.09	0.06- 0.11	0.19	0.12-0.23	0.0023
Pink salmon	9	0.10	—	0.28	0.21-0.31	0.0062
Chum salmon	4	0.10	—	0.31	0.30-0.33	0.0075
Tintinnids:						
Clarke-Bumpus sampler	1	0.25	—	0.14	—	0.0038
Pink salmon	—	—	—	—	—	—
Chum salmon	—	—	—	—	—	—
Hydromedusans:						
Clarke-Bumpus sampler	2	0.18	—	0.31	—	0.0136
Pink salmon	—	—	—	—	—	—
Chum salmon	—	—	—	—	—	—
Rotifers:						
Clarke-Bumpus sampler	9	0.24	0.18- 0.31	0.16	0.11-0.20	0.0048
Pink salmon	8	0.32	0.30- 0.36	0.19	0.16-0.23	0.0091
Chum salmon	2	0.32	0.31- 0.33	—	—	0.0091
Gastropods (veligers):						
Clarke-Bumpus sampler	1	0.20	—	0.14	—	—
Pink salmon	8	0.38	0.30- 0.75	0.28	0.20-0.40	0.0234
Chum salmon	1	0.68	—	0.44	—	0.1034
Pelecypods (veligers):						
Clarke-Bumpus sampler	4	0.28	0.19- 0.40	0.18	0.15-0.21	0.0071
Pink salmon	12	0.34	0.22- 0.47	0.31	0.22-0.39	0.0257
Chum salmon	6	0.35	0.28- 0.38	0.32	—	0.0281
Polychaetes (larvae):						
Clarke-Bumpus sampler	2	0.46	0.38- 0.50	0.17	0.13-0.21	0.0104
Pink salmon	11	0.94	0.61- 1.60	0.24	0.19-0.30	0.0425
Chum salmon	10	2.04	1.01- 4.00	0.29	0.28-0.47	0.1347
Arachnids:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	1.20	—	1.20	—	1.3572
Chum salmon	9	1.38	0.30- 1.80	1.38	0.18-3.50	2.0841
Crustaceans (nauplii):						
Clarke-Bumpus sampler	11	0.30	0.23- 0.40	0.14	0.10-0.19	0.0046
Pink salmon	7	0.37	0.28- 0.45	0.17	—	0.0084
Chum salmon	7	0.45	0.30- 0.60	0.21	—	0.0156
Cladocerans:						
Clarke-Bumpus sampler	11	0.50	0.31- 0.71	0.28	0.20-0.35	0.0308
Pink salmon	20	0.62	0.32- 0.91	0.33	0.17-0.46	0.0530
Chum salmon	21	0.60	0.28- 1.10	0.32	—	0.0482
Copepods:						
Clarke-Bumpus sampler	13	0.62	0.40- 1.23	0.19	0.12-0.30	0.0176
Pink salmon	99	1.00	0.26- 3.20	0.37	0.10-1.12	0.1075
Chum salmon	62	1.12	0.30- 3.30	0.41	0.11-1.10	0.1479
Cirripedes (nauplii):						
Clarke-Bumpus sampler	24	0.39	0.28- 0.61	0.22	0.16-0.42	0.0148
Pink salmon	28	0.47	0.28- 0.87	0.29	0.17-0.50	0.0310
Chum salmon	10	0.55	0.30- 1.20	0.34	0.16-0.56	0.0499
Cirripedes (cyprids):						
Clarke-Bumpus sampler	1	0.53	—	0.28	—	0.0326
Pink salmon	16	0.85	0.60- 1.00	0.37	0.25-0.46	0.0914
Chum salmon	14	0.84	0.62- 1.00	0.37	0.27-0.46	0.0903
Mysids:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	2.10	—	0.25	—	0.1031
Chum salmon	—	—	—	—	—	—
Cumaceans:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	2	1.80	1.50- 2.10	0.46	—	0.2991
Chum salmon	3	2.11	1.52- 2.90	0.54	—	0.4832
Isopods:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	0.76	—	0.50	—	0.1492
Chum salmon	3	0.62	0.52- 0.80	0.31	0.26-0.40	0.0468
Amphipods:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	1.48	—	0.59	—	0.4046
Chum salmon	3	1.05	0.90- 1.25	0.42	—	0.1455
Euphausiids:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	3	2.67	2.50- 2.70	0.48	—	0.4832
Chum salmon	1	2.70	—	0.48	—	0.5092

TABLE 5.—Continued.

Item and place collected	Number measured	Length (mm)		Diameter (mm)		Average volume (mm³)
		Average	Range	Average	Range	
Decapods (zoeae)						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	10	1.79	0.94- 5.80	0.39	0.12-1.27	0.2138
Chum salmon	10	2.05	1.28- 3.04	0.45	0.28-0.67	0.3760
Collembolans						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	—	—	—	—	—	—
Chum salmon	14	1.57	0.87- 1.94	0.41	0.30-0.50	0.2573
Dipterans (larvae)						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	3	1.43	1.25- 1.60	0.13	0.11-0.14	0.0190
Chum salmon	8	2.96	1.45- 4.00	0.27	0.13-0.37	0.1665
Dipterans (pupae)						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	2.30	—	0.36	—	0.2300
Chum salmon	21	1.80	1.25- 2.80	0.43	0.27-0.70	0.2614
Dipterans (adults)						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	—	—	—	—	—	—
Chum salmon	4	2.58	1.65- 3.30	0.39	0.24-0.52	0.2882
Unidentified insect remains						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	—	—	—	—	—	—
Chum salmon	—	0.52	—	—	—	0.0614
Larvaceans						
Clarke-Bumpus sampler	1	0.20	—	0.14	—	0.0031
Pink salmon	9	0.89	0.50- 1.05	0.39	0.28-0.60	0.1499
Chum salmon	30	0.69	0.41- 1.30	0.39	0.23-0.74	0.1499
Polyzoans						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	0.60	—	0.19	—	0.0032
Chum salmon	—	—	—	—	—	—
Eggs (invertebrate)						
Clarke-Bumpus sampler	7	—	—	0.32	0.20-0.40	0.0172
Pink salmon	11	—	—	0.31	0.11-0.40	0.0156
Chum salmon	16	—	—	0.34	0.10-0.42	0.0206
Eggs (vertebrate)						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	5	—	—	0.88	0.80-0.96	0.3566
Chum salmon	1	—	—	0.80	—	0.2210
Fish						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	3	5.67	4.85- 6.00	0.14	—	0.0873
Chum salmon	3	16.70	15.00-20.00	0.42	—	2.3137

Stomach Evacuation

The time required for satiated fry in the aquarium to evacuate food in their stomachs was inversely related to temperature. In tests at 12.8°C, the stomachs of two of five pink salmon were empty after 2 h without food. However, 6 h elapsed before successive samples of five fish contained no food, and 6 h was therefore accepted as the time required for pink salmon to evacuate their stomachs at a temperature of 12.8°C (Table 6). For chum salmon, the first empty stomach was observed after 1 h without food at 12.8°C. Only after 10 h did successive samples of five chum salmon have empty stomachs. This longer evacuation time for chum salmon probably resulted from the larger and different kinds of organisms eaten. Using the same criterion for time of evacuation as described above for 12.8°C, pink salmon fry confined without food had empty stomachs after 9 h at 10°C and after 16 h at 8.5°C. We did not test chum salmon at the lower temperatures.

TABLE 6.—Time required for pink and chum salmon fry to evacuate food from their stomachs at various temperatures.

Temperature (°C)	Pink salmon (hours)	Chum salmon (hours)
8.5	16	—
10.0	9	—
12.8	6	10

ZOOPLANKTON ABUNDANCE AND DISTRIBUTION

The abundance of zooplankton in the near-surface waters was determined from the samples we collected in the inner and outer bays of Traitors

Cove in June 1965 and in April, May, and June 1966 when salmon fry were present. The lowest abundance in the inner bay, an average of 9 organisms per liter, occurred in April 1966, when the abundance was comparatively high in the outer bay, 51 per liter (Table 7). During the rest of the 1966 season, mean numbers ranged from 27 to 28 organisms per liter in the inner bay and 24 to 40 in the outer bay. The highest numbers were observed in the outer bay in June 1965 after most of the fry had passed through the estuary. Zooplankters tended to be more abundant at the mouth of the bay, near the constriction, and at the head of the bay than at intervening points along the shoreline.

Fifty-two categories of zooplankters were identified from the Clarke-Bumpus samples, and seasonal qualitative and quantitative changes were evident in the composition of the zooplankton (Table 8). The peak abundance for polychaete larvae and cirripede (barnacle) nauplii occurred in April, whereas the peak for other invertebrate larvae occurred in May. Rotifers, copepods (including nauplii), and barnacle nauplii were also very abundant in May. Cladocerans did not become abundant until June. Variation between years is indicated by the high abundance of rotifers in June 1965 (~120,000/m³) and the much lower abundance of rotifers (~3,000/m³) and possibly higher abundance of other forms in June 1966.

The predominant zooplankters during the period of fry outmigration were larvae of barnacles, polychaetes, and molluscs and nauplii and early copepodites of the copepods *Acartia clausii*, *A. longiremis*, and *Oithona helgolandica*. Over 90% of the zooplankters in the outer bay on 16 April 1966 were larvae, and as late as 7 June 1966 larvae constituted more than 65% of the zooplankton. In the inner bay on 18 April 1966 and 7 June 1966, the proportions of larvae in the zooplankton were 72 and 58%, respectively. Late copepodites and adults of calanoid and cyclopoid copepods were the next most abundant groups of zooplankters and contributed relatively more to the zooplankton as the season progressed. An abundance of larval forms was also characteristic of another southeastern Alaska estuary, Auke Bay (Wing and Reid 1972). Rotifers, although of minor importance in the diet of salmon fry, were often the most abundant zooplankters in the samples. Cladocerans and larvaceans were rare in April and May but by June constituted a significant portion of the zooplankton. Adults and juveniles of benthic invertebrates were rare in the plankton samples. Species composition of zooplankters differed between the inner and outer bays of Traitors Cove (Table 8).

TABLE 7.—Abundance of zooplankters determined from Clarke-Bumpus sampler with no. 10 mesh net (158 μm) at Traitors Cove.

Date	Inner bay			Outer bay		
	Number of samples	Organisms per liter		Number of samples	Organisms per liter	
		Mean	Range		Mean	Range
16 June 1965	—	—	—	7	104	8-583
16-18 Apr. 1966	15	9	1-28	14	51	6-180
16 May 1966	10	28	2-70	14	24	10-44
7 June 1966	10	27	2-62	14	40	4-85

The plankton samples contained zooplankton of the kinds and sizes eaten in great numbers by pink and chum salmon fry as well as smaller plankters, which were not important in the diet of fry. As a result, the average size of plankters in the net was slightly smaller than the average size of items eaten (Table 5).

DISCUSSION

Initiation of Feeding

Neither pink nor chum juvenile salmon ate very much before leaving Traitors River, although chum salmon fed more than pink salmon. Some fry may have fed before they emerged from the redds. The size (41 mm) of the largest fry collected in the river suggests that at least a few individuals actually grew as a result of exogenous feeding before they finally left the river. Mason (1974) collected chum salmon fry up to 70 mm long from Lymn Creek on Vancouver Island, British Columbia, where they moved into and out of high-salinity water and apparently fed in both media over a period of 1 to 4 wk or more.

Immature stages of chironomids were most commonly eaten, but other bottom-dwelling aquatic organisms also occurred in stomachs of pink and chum salmon from Traitors River. Two workers (Disler 1953; Sparrow 1968) reported that zooplankton and bottom-dwelling aquatic organisms occurred in the diet of chum salmon in freshwater. Although pink salmon apparently eat little or nothing while migrating seaward in short streams (Kazarnovskii 1962; Kobayashi 1968), as at Traitors River, they are more likely to feed while migrating long distances from large rivers (Levanidov and Levanidova 1957; McDonald 1960).

Once they had left the stream, pink and chum salmon fry in Traitors Cove fed extensively on such zooplankters as calanoid copepods, lar-

TABLE 8.—Average species composition of zooplankton samples during salmon fry outmigration at Traitors Cove, June 1965 and April to June 1966. (See Table 4 for number of samples. Numbers of zooplankters per cubic meter rounded to nearest whole number. Percentages rounded to 0.1%; + indicates less than 0.5%.)

Item	Inner bay						Outer bay							
	18 Apr. 1966		16 May 1966		7 June 1966		16 June 1965		16 Apr. 1966		16 May 1966		7 June 1966	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Hydromedusans:														
Bougainvillia sp.	—	—	1	+	—	—	—	—	—	—	2	+	—	—
Obelia sp.	4	+	26	+	—	—	17	+	—	—	5	+	—	—
Phialidium sp.	—	—	2	+	—	—	—	—	—	—	1	+	—	—
Sarsia tubulosa (M. Sars)	—	—	1	+	—	—	—	—	—	—	1	+	45	+
Unidentified	2	+	—	—	—	—	15	+	—	—	—	—	—	—
Ctenophores:														
Pleurobrachia pileus (Müller)	—	—	1	+	—	—	—	—	—	—	—	—	—	—
Nemertines (pilidium)	—	—	—	—	—	—	—	—	—	—	3	+	—	—
Rotifers	930	10.0	1,523	5.4	229	0.8	124,870	80.9	10	+	1,514	6.4	2,802	6.8
Bryozoans (cyphonautes)	10	+	30	+	—	—	—	—	—	—	108	+	96	+
Molluscs:														
Littorina scutulata Gould (egg cases)	—	—	41	+	107	+	36	+	8	+	280	1.2	46	+
Gastropoda (veligers)	221	2.4	345	1.2	84	+	52	+	102	+	127	0.5	—	—
Pelecypoda (veligers)	716	7.7	1,008	3.6	139	0.5	122	+	22	+	694	2.9	1,929	4.7
Polychaetes (larvae)	1,370	14.8	686	2.4	—	—	62	+	891	1.7	547	2.3	205	0.5
Tardigrades	2	+	—	—	—	—	—	—	—	—	—	—	—	—
Cladocerans:														
Evadne nordmanni Loven	2	+	4	+	—	—	419	+	4	+	6	+	—	—
Podon leuckarti Sars	—	—	3	+	—	—	670	+	—	—	3	+	—	—
Unidentified	—	—	—	—	1,096	3.8	—	—	—	—	—	—	2,104	5.1
Ostracods	—	—	1	+	—	—	—	—	—	—	—	—	—	—
Copepods (late copepodites and adults):														
Acartia clausi Giesbrecht	8	+	780	2.8	—	—	3,087	2.0	2	+	47	+	—	—
A. longiremis (Lilljeborg)	17	+	723	2.6	—	—	336	+	110	+	148	0.6	—	—
Acartia spp.	79	0.9	4,571	16.2	—	—	4,486	2.9	46	+	2,852	12.1	—	—
Calanus finmarchicus (Gunnerus)	—	—	386	1.4	—	—	—	—	—	—	158	0.7	—	—
Centropages abdominalis Sato	—	—	—	—	—	—	—	—	—	—	8	+	—	—
Metridia sp.	2	+	166	0.6	—	—	—	—	2	+	111	+	—	—
Pseudocalanus minutus (Krøyer)	84	0.9	1,621	5.8	—	—	95	+	143	+	862	3.6	—	—
Tortanus discaudatus (Thompson and Scott)	1	+	16	+	—	—	—	—	—	—	6	+	—	—
Calanoida spp.	14	+	—	—	—	—	81	+	—	—	1	+	—	—
Oithona helgolandica Claus	486	5.2	687	2.4	—	—	981	0.6	466	0.9	514	2.2	—	—
Cyclopoida spp.	58	0.6	169	0.6	—	—	—	—	7	+	136	0.6	—	—
Harpacticoida spp.	58	0.6	14	+	—	—	34	+	2	+	21	+	—	—
Unidentified	—	—	—	—	10,422	36.5	—	—	—	—	—	—	9,201	22.4
Copepods (nauplii)	1,980	21.4	10,237	36.3	—	—	9,972	6.5	909	1.8	4,264	18.0	—	—
Cirripedes (nauplii)	2,334	25.2	4,041	14.3	10,281	36.0	6,994	4.5	48,067	93.9	9,714	41.1	13,706	33.4
Cirripedes (cyprids)	—	—	236	0.8	131	+	70	+	—	—	893	3.8	92	+
Cumaceans:														
Cumella vulgaris Hart	1	+	—	—	—	—	—	—	—	—	—	—	—	—
Amphipods:														
Corophiidae	—	—	1	+	50	+	—	—	—	—	—	—	—	—
Euphausiids (calyptopis)	—	—	—	—	—	—	—	—	—	—	10	+	—	—
Euphausiids (nauplii)	99	1.1	429	1.5	—	—	—	—	206	+	166	0.7	—	—
Carids (zoeae)	—	—	—	—	—	—	—	—	2	+	1	+	—	—
Brachyurans (zoeae)	—	—	16	+	—	—	—	—	—	—	7	+	—	—
Pagurians (zoeae)	—	—	—	—	—	—	—	—	3	+	—	—	—	—
Crustaceans (nauplii):														
Unidentified	—	—	—	—	5,855	20.5	—	—	6	+	1	+	10,418	25.4
Chaetognaths:														
Sagitta elegans Verrill	4	+	2	+	—	—	—	—	9	+	—	—	—	—
Echinoderms:														
Echinoplutei	4	+	32	+	—	—	—	—	1	+	19	+	—	—
Bipinnaria	—	—	—	—	—	—	—	—	—	—	3	+	—	—
Tunicates:														
Fritillaria borealis Lohmann	5	+	12	+	—	—	—	—	8	+	—	—	—	—
Oikopleura sp.	—	—	—	—	—	—	—	—	11	+	—	—	92	+
Tunicata (larvae)	—	—	—	—	—	—	107	+	2	+	—	—	—	—
Tunicata (eggs)	—	—	20	+	—	—	12	+	33	+	—	—	—	—
Unidentified invertebrate larvae	17	+	39	+	—	—	51	+	9	+	15	+	—	—
Unidentified invertebrate eggs	764	8.2	309	1.1	—	—	1,765	1.1	86	+	370	1.6	—	—
Fish larvae	—	—	—	—	—	—	—	—	1	+	1	+	—	—
Fish eggs	—	—	5	+	—	—	—	—	—	—	—	—	362	0.9
Total	9,272	—	28,177	—	28,563	—	154,348	—	51,159	—	23,630	—	41,091	—

[1]No sampling was done in the inner bay in 1965.
[2]June 1966 samples were not available for taxonomic breakdown.

vaceans, barnacle nauplii, cladocerans, and other small crustaceans. Chum salmon fry tended to eat more larger hard-shelled organisms and epibenthic organisms than did pink salmon fry. The food of pink and chum salmon fry at Traitors Cove in general was similar to that reported at Uala and Anapka bays on the east side of the Kamchatka Peninsula (Andrievskaya 1968), the San Juan area of northern Washington (Annan 1958), the Strait of Georgia in southern British Columbia (Barraclough 1967; Robinson et al. 1968), Chatham Sound off the northern coast of British Columbia (Manzer 1969), and Moser Bay of southeastern Alaska (Chamberlain 1907). In contrast, in Puget Sound epibenthic organisms (especially harpacticoid copepods) were more important than pelagic zooplankters to pink and chum salmon fry (Gerke and Kaczynski 1972).

Food Selection

Salmon fry in Traitors Cove did not eat the same kinds and sizes of zooplankters in the same relative numbers as they appeared in the samples of zooplankton, i.e., the fry fed selectively. Selective feeding in relation to sizes of prey and juvenile chum salmon has been reported by LeBrasseur (1969). The average size of the zooplankton eaten by the fish was greater than the zooplankton collected by the Clarke-Bumpus sampler (Table 5). A coarser net such as a no. 6 mesh (233 µm) would probably have collected the zooplankters that were usually eaten by salmon fry and would not have collected so many of the small forms that are seldom eaten such as tintinnids, rotifers, and others.

Selective feeding by pink and chum salmon fry was also demonstrated by the occurrence of certain food items relatively more often in the stomachs of fry (Tables 3, 4) than in the plankton samples (Table 8). Relatively more cladocerans, decapod zoeae, and larvaceans were eaten by salmon than appeared in the plankton samples. Another example of the marked disparity is the barnacle nauplii which were very abundant in most of the plankton samples (4 to 94% of the number of plankters) but constituted only 14% of the animals actually eaten by pink salmon and only 3% of the number of food items eaten by chum salmon.

The high incidence of larvaceans in the stomach samples, especially in the chum salmon, may be the result of selective feeding on a scarce but very visible plankter. Larvaceans, in particular *Oikopleura* spp., form mucous feeding nets which may increase the visibility of the larvacean to the salmon fry. Once learning to capture *Oikopleura*, the fry may prefer that food item.

Benthic and intertidal forms of mysids, cumaceans, isopods, amphipods, and insects were rare in the plankton samples and their presence in some of the stomachs shows that pink and chum salmon fry did on occasion feed in these ecological niches. This type of feeding behavior could not predominate at Traitors Cove because most of the shoreline is rocky and precipitous and offers little opportunity for benthic feeding.

Grazing Rate

The average number of zooplankters consumed daily by a pink salmon fry in Traitors Cove was calculated from estimates of average stomach contents and evacuation rates. Stomachs of pink salmon collected from Traitors Cove estuary during daylight contained an average of 136 zooplankters. Stomach evacuation required 6 and 16 h at temperatures of 12.8°C and 8.5°C, respectively, although Brett and Higgs (1970) observed slower stomach evacuation rates at comparable temperatures in sockeye salmon fingerlings that had been fed a commercial pelleted food. The fry did not feed during darkness, which extended from about one-half hour after sunset to one-half hour before sunrise on cloudy or moonless nights. The duration of feeding at Traitors Cove when fry are present typically is about 16.5 h (range 15 to 18 h); the water temperature at 1 m ranges from 5° to 13°C.

Thus, it appears that fry would consume a volume of food required to fill their stomachs once a day at cooler temperatures (8.5°C) and four times a day at warmer temperatures (12.8°C). The number of zooplankters consumed daily would, therefore, range between 136 and 544 per pink salmon fry for temperatures that are normal during the time fry are in Traitors Cove. By the same line of reasoning, chum salmon would consume about 120 to 480 food items per fry per day in Traitors Cove.

Some insight into the availability of food for salmon fry at Traitors Cove was obtained by considering the abundance of plankton in relation to the feeding habits of the fry. For example, fry 39 mm long that were holding a position relative to the shore while feeding in a current of 11 cm/s were in effect grazing a cylindrical mass of water at the rate of about 3.5 liter/min. Even at the lowest observed abundance of 1 zooplankter per liter (Table 5), each fry would theoretically encounter about 3.5 zooplankters per minute, which is slightly greater than the estimated feeding rate of 3 zooplankters per minute in floating aquaria at 10°C. At this rate of feeding, a single fry could fill its stomach in about 39 to 155 min and could therefore easily ingest zooplankters faster than they could be evacuated.

Abundance of zooplankton in the outer bay of Traitors Cove ranged from 4 to 563 organisms per liter (Table 7), and this was theoretically enough to satiate feeding fry as shown above. Furthermore, the abundance of zooplankton as estimated from Clarke-Bumpus samples did not decrease during the time that salmon fry were in the estuary. Therefore, we conclude that there was an abundant food supply in Traitors Cove for salmon fry. LeBrasseur et al. (1969), who conducted feeding experiments with wild juvenile pink and chum salmon in the Fraser River estuary in 1967 (an off-cycle year of pink salmon in the Fraser system), arrived at a similar conclusion for that area.

Carrying Capacity of Traitors Cove

Fry of pink and chum salmon emerged from the gravel of Traitors River at night, and most of them migrated to the estuary before dawn. Some of the fry, as evidenced by their size and the contents of their digestive tracts, lingered a few days in the stream where they fed on freshwater organisms. The tendency to linger and feed in freshwater, most pronounced for chum salmon, has been described by Mason (1974). After the fry left Traitors River, they gathered in schools close to shore and began feeding and migrating oceanward. The time spent in the estuary is unknown but was probably from a few days to a few weeks.

We estimated the abundance of pink and chum salmon fry in Traitors Cove by making counts each day along the shore from a moving skiff or by a mark-and-recapture technique. In 1965, the greatest number estimated from counts on any day was 7 million fry, but in 1966 the greatest estimate was under 1 million fry. The number of salmon fry in Traitors Cove in 1968 was estimated by mark and recapture to be 4 million (±1.3 million, 95% confidence limits). The mark-and-recapture estimate was made on a different annual fry migration than those covered by this study of feeding habits, but it strengthened our confidence in the visual estimates of fry abundance in 1965 and 1966.

It did not appear that the Traitors Cove estuary was overgrazed by wild fry at the time of this study. In 1966, zooplankton abundance was always greater than 1.0 zooplankter per liter, which would allow maximum feeding rates by fry. During May and June 1966, when 1 million fry were present, the average abundance was about 29 zooplankters per liter. In June 1965, abundance was 154 zooplankters per liter after 7 million fry passed through the estuary.

The number of fry that migrate through Traitors Cove each year is probably limited to less than 20 million by the productivity of the spawning grounds in Traitors River and Margaret Creek, the major salmon streams in the cove. We used stream survey data from Martin (1959) and applied a correction factor of 0.5 to correct for pools and stream bottoms of mud, sand, and bedrock to calculate 66,000 m² of spawning grounds—55,000 m² in Traitors River and 11,000 m² in Margaret Creek. These spawning grounds would yield about 7 million fry if they produced 100 fry per square meter or about 20 million fry if they produced 300 fry per square meter. Fry densities of 0.1 to 509 per square meter (average 250 fry per square meter) have been observed in Traitors River,[illegible] but these densities were in sections of the stream consistently favored by spawning salmon. Less favored areas were not sampled.

The installation of a hatchery or spawning channel in a drainage system such as Traitors River could potentially result in a production of 100 million fry annually, or 5 to 100 times the estimated production of wild fry. Available data are inadequate to determine the carrying capacity of Traitors Cove with certainty, but it is possible to make very speculative estimates based on the standing crop of zooplankton.

Before presenting the estimates of carrying capacity, we wish to cite 10 necessary assumptions (required because we lack knowledge of the ecology of estuarine nursery areas) and some of the factors which may invalidate the estimates.

1. Zooplankton abundance was the same in Behm Canal as in Traitors Cove. Plankton samples

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[illegible] Mattson, C. R., and J. E. Bailey. 1966. Chum and pink salmon studies at Traitors Cove, September 1963 to September 1964. On file, Auke Bay Laboratory.

[illegible] Mattson, C. R., and R. G. Rowland. 1963. Chum salmon studies at Traitors Cove Field Station June 1960 to March 1963. On file, Auke Bay Laboratory.

were not collected outside Traitors Cove in Behm Canal. Several years later extensive plankton collections were made in open channels and several small adjacent bays of northern southeastern Alaska as a part of the 1972 MARMAP[3] investigation. Within the May 1972 samples, average zooplankton abundance was nearly twice as great at 14 outside stations as at 4 stations within bays. Therefore, our estimates of carrying capacity based on influx of zooplankton from Behm Canal would be conservative.

2. Salmon fry were the only predators on zooplankton. We ignored the requirements of all other planktivorous animals of the area. The requirement of local planktivores other than salmon are only qualitatively and poorly known. Herring were not seen in large numbers during the years of this food study. A school of herring entered the inner bay in 1967 while being fed on by a whale. We do not know how long these herring remained in Traitors Cove, but they were not conspicuous 2 wk after their entry.

3. Zooplankton concentrations were constant. We ignored the strong seasonality of reproduction and growth in the holoplankton and the fact that meroplankton may be present for only a limited time. We ignored the probability that some larval forms reach a life history stage where their behavior would make them unavailable to the salmon fry. We ignored natural mortality of larval forms other than from predation by salmon fry. Some of these factors would increase zooplankton concentrations while others would decrease them. In the absence of information on reproduction, growth, mortality, and life histories, we assumed these factors would balance so that the zooplankton concentration would be constant.

4. Distribution of the zooplankton was uniform. Physical and biological factors controlling the patchiness of zooplankton in estuaries and nearshore environments are poorly understood and not easily modeled.

5. All zooplankton were equally available, equally desirable, and of equal quality as feed for salmon fry. We ignored the size selectivity and preference for calanoid copepods shown in our own data. It is highly probable that the species of zooplankton vary in quality as food.

6. Salmon fry had a constant feeding requirement of 544 zooplankters per day. This is the highest of our estimates of pink salmon feeding rates and ignores variations in food requirements that would accompany variations in physical environment and physiological state.

7. No behavioral changes in either the salmon fry or zooplankton were induced by changes in densities, physical environment, or biological states.

8. The number of salmon fry was constant.

9. All the zooplankton would be utilized as food. If this actually occurred, no survivors would be left to produce new zooplankton crops or to replenish stocks of other resources that have planktonic larval stages such as herring, crabs, and shrimp.

10. Models of circulation in the estuary would be of the simplest type. We do not know the flushing rates in Traitors Cove or the potential of transport of zooplankton food to and from the bay by estuarine circulation.

Some additional assumptions peculiar to each estimate are described with each estimate. Only the outer bay is considered because fry in Traitors Cove appeared to move quickly through the inner bay and then spend a longer time in the outer bay.

Our first estimate of carrying capacity is based on standing stock of zooplankton in the top meter of water of the outer bay. Fry were in the outer bay in relatively high densities for about 30 days each year. The surface area of the outer bay is about 7.6×10^6 m^2, and the average density of zooplankters was estimated to be 24,000 per cubic meter or higher. The product of area and plankton density divided by 544 (the estimated maximal number of organisms consumed per day by pink salmon fry) results in a plankton stock equivalent to 335×10^6 fry feeding days. This estimate divided by 30 days expresses the food supply in fry months–11 million fry could feed for 1 mo on the standing stock of food in the surface meter of outer bay. This establishes a lower limit for the carrying capacity of Traitors Cove because it ignores saltwater entrainment by outflowing freshwater and the consequent addition of plankton from deeper water.

For our second estimate, we calculated the quantity of zooplankton that would be brought into the outer bay from Behm Canal each day by a combination of two factors: circulation due to freshwater runoff from Traitors River and circulation due to tidal action. Records of the U.S. Geological Survey indicate that discharge from Traitors River generally averages about 8 m^3/s in the spring when fry are migrating. Assuming an equal flow of seawater with plankton density of 24,000 organisms per cubic meter into Traitors Cove from Behm Canal and surface entrainment near the constriction, we calculated that 16.5×10^9 organisms would be brought daily into Traitors Cove by freshwater-driven circulation. Dividing the number of organisms by 544 (the high estimate of organisms eaten by one fry daily) yields a conservative estimate of 30 million fry that could be fed by an amount of food added daily by circulation. Although it is naive to assume that all of the plankton brought into Traitors Cove as a result of circulation would become available to the fry, the upwelling and thorough mixing that occur at the constriction between the two bays result in a continual resupplying of zooplankton to the upper meter of depth where grazing apparently takes place. Field observations did indicate that the largest concentrations of fry were consistently found in eddies near the constriction, lending some credence to the theory that upwelling of deep water created a favorable supply of food in this area.

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[3] Marine Resources Monitoring, Assessment, and Prediction–program sponsored by National Marine Fisheries Service on a nationwide scale.

The effects of tidal circulation and freshwater-runoff-driven circulation are often additive. Therefore, we calculated the influx of food organisms by tidal exchange. We assumed that the surface waters were flushed completely by the outgoing tide; that complete mixing of incoming water with water present occurred on each tide; and that all zooplankton in the upper meter had been consumed before the waters were mixed. The influx of new food can then be estimated from the tidal prism as

$$F = [T/V] \times P$$

where F is the net influx of new food organisms as zooplankters per cubic meter per tide; T is the volume of the tidal prism; V is the volume of the outer bay; and P is the density of zooplankton outside the bay. (We used $P = 24 \times 10^3/\mathrm{m}^3$ because we assumed that abundance was the same outside the bay as it was inside.)

The resulting calculation assuming a mean tidal range of 4.11 m (McLain 1968) and a mean depth of 90 m gives for the net influx of organisms per tide:

$$F = \frac{4.11\ \mathrm{m/tide}}{90\ \mathrm{m}} \times 24 \times 10^3/\mathrm{m}^3 = 1.09 \times 10^3 \text{ zooplankters per cubic meter per tide.}$$

Only those in the upper meter are available, and since there are two tides per day, the calculated quantity of new food available to salmon fry per day is:

$$\begin{aligned} Q &= 2 \times F \times [\text{area of bay}] \times 1\ \mathrm{m} = 2\ \text{tides/day}\ (1.09 \times 10^3 \text{ zooplankton per cubic meter per tide}) \times (7.6 \times 10^6\ \mathrm{m}^2 \times 1\mathrm{m}) \\ &= 16.6 \times 10^9 \text{ zooplankters per day.} \end{aligned}$$

This number will feed 30×10^6 fry per day (16.6×10^9 zooplankters ÷ 544 zooplankters per day per fry). The estimate is high because mixing is not complete, as implied by the calculations. By adding fry that could be fed from the effects of freshwater runoff to fry that could be fed by tidal action, we get an upper estimate of carrying capacity of 60 million fry.

The numbers of fry that could theoretically be fed by the two sources of zooplankton, i.e., standing crop in the surface water and plankton in the net circulation, are not strictly additive. Although some plankton in deep seawater would be continuously entrained upward to flow seaward on the surface, some would never reach the surface of the bay and a portion of the surface stock would be removed from the bay by outflow. Therefore, it would seem prudent to consider that populations numbering more than 30 million pink and chum salmon fry might cause reduced growth of fry (because of the competition for food). Also, such large populations might stimulate a more rapid migration of fry through the estuary to areas where food organisms were more abundant.

On the basis of available spawning grounds, it seems unlikely that Traitors Cove has ever had to support more than 20 million pink and chum salmon fry, although it is possible that 11 to 60 million fry could be supported in years when food abundance equaled or exceeded that observed in 1966. The release of 50 to 100 million additional hatchery fry into this estuary would probably exceed the carrying capacity of the area. Competition for food, especially if zooplankton production were lower than average, and increased potential infection by disease, parasitism, and predation could theoretically result in increased mortality, slower growth, or accelerated movement of fry out of the estuary. Further, a great increase in numbers of salmon fry in Traitors Cove could deplete planktonic food and planktonic larvae required to support other fisheries. We have used Traitors Cove to discuss carrying capacity of estuaries only because observations on fry and food were available. We know of no plans for the operation of a hatchery in Traitors Cove. The discussion is merely intended to focus attention on an important factor to be considered in choosing sites and operating salmon fry hatcheries.

LITERATURE CITED

ANDRIEVSKAYA, L. D.
1968. Feeding of Pacific salmon fry in the sea. [In Russ.] Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 64:73-80. (Translated by Transl. Bur., Dep. Secretary of State of Canada, 1970, 16 p.)

ANNAN, M. E.
1958. Notes on the food of the young of three species of Pacific salmon in the sea. Can. Fish Cult. 23:23-25.

BAILEY, J. E., AND W. R. HEARD.
1973. An improved incubator for salmonids and results of preliminary tests of its use. U.S. Dep. Commer., NOAA Tech. Memo. NMFS ABFL-1, 7 p.

BAILEY, J. E., AND S. G. TAYLOR.
1974. Salmon fry production in a gravel incubator hatchery, Auke Creek, Alaska, 1971-72. U.S. Dep. Commer., NOAA Tech. Memo. NMFS ABFL-3, 13 p.

BAMS, R. A.
1972. A quantitative evaluation of survival to the adult stage and other characteristics of pink salmon (*Oncorhynchus gorbuscha*) produced by a revised hatchery method which simulates optimal natural conditions. J. Fish. Res. Board Can. 29:1151-1167.

BARRACLOUGH, W. E.
1967. Number, size and food of larval and juvenile fish caught with a two boat surface trawl in the Strait of Georgia April 25-29, 1966. Fish. Res. Board Can., Biol. Stn. Nanaimo, B.C., Manuscr. Rep. Ser. 922, 54 p.

BRETT, J. R., AND D. A. HIGGS.
1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. 27:1767-1779.

CHAMBERLAIN, F. M.
1906. Some observations on salmon and trout in Alaska. Rep. U.S. Comm. Fish., 1906 (Doc. 627), 112 p.

CUSHING, C. E., JR.
1961. A plankton subsampler. Limnol. Oceanogr. 6:489-490.

DISLER, N. N.
1953. Ecological and morphological characteristics of the development of the Amur autumn chum salmon—*Oncorhynchus keta* (Walb.). [In Russ.] Tr. Soveshch. Ikhtiol. Kom., Akad. Nauk SSSR 1:354-362. (Translated by Israel Program Sci. Transl., 1961; *In* Pacific salmon, selected articles from Russian periodicals, p. 33-41; available U.S. Dep. Commer., Off. Tech. Serv., Wash., D.C., as OTS 60-51139.)

FRASER, F.
1972. Evaluation of chum spawning channels (Abstr.). *In* J. E. Bailey (editor), Proceedings of the 1972 northeast Pacific pink salmon workshop, p. 55-64. Alaska Dep. Fish Game, Inf. Leafl. 161.

GERKE, R. J., AND V. W. KACZYNSKI.
1972. Food of juvenile pink and chum salmon in Puget Sound, Washington. Wash. Dep. Fish., Tech. Rep. 10, 27 p.

HOAR, W. S.
1942. Diurnal variations in feeding activity of young salmon and trout. J. Fish. Res. Board Can. 6:90-101.

IVANKOV, V. N., AND A. P. SHERSHNEV.
1968. (Biology of juvenile pink salmon and chum salmon in the sea.) [In Russ.] Rybn. Khoz. 44:16-17.

KANID'YEV, A. N., G. M. KOSTYUNIN, AND S. A. SALMIN.
1970. Hatchery propagation of the pink and chum salmons as a means of increasing the salmon stocks of Sakhalin. J. Ichthyol. 10:249-259.

KAZARNOVSKII, M. YA.
1962. Food of migrating fry of *Oncorhynchus gorbuscha* and *Salvelinus malma* in the rivers of Sakhalin. [In Russ.] Rybn. Khoz. 38(6):24-25. (Abstr. translated from Russ. in Biol. Abstr. 41(20082).)

KOBAYASHI, T.
1965. A note on the seaward migration of pink salmon fry. [In Jap., Engl. summ.] Sci. Rep. Hokkaido Salmon Hatchery 22:1-5.

LEBRASSEUR, R. J.
1969. Growth of juvenile chum salmon (*Oncorhynchus keta*) under different feeding regimes. J. Fish. Res. Board Can. 26:1631-1645.

LEBRASSEUR, R. M., W. E. BARRACLOUGH, O. D. KENNEDY, AND T. R. PARSONS.
1969. Production studies in the Strait of Georgia. Part III. Observations on the food of larval and juvenile fish in the Fraser River plume, February to May, 1967. J. Exp. Mar. Biol. Ecol. 3:51-61.

LEVANIDOV, V. Y., AND I. M. LEVANIDOVA.
1957. Food of downstream migrating young summer chum salmon and pink salmon in Amur tributaries. [In Russ.] Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 45:3-16. (Translated by Israel Program Sci. Transl., 1961; *In* Pacific salmon, selected articles from Russian periodicals, p. 269-284; available U.S. Dep. Commer., Off. Tech. Serv., Wash., D.C., as OTS 60-51139.)

MANZER, J. I.
1969. Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. J. Fish. Res. Board Can. 26:2219-2223.

MARTIN, J. W. (editor)
1959. Stream catalog of eastern section of Ketchikan management district of southeastern Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 305 [615 p.].

MASON, J. C.
1974. Behavioral ecology of chum salmon fry (*Oncorhynchus keta*) in a small estuary. J. Fish. Res. Board Can. 31:83-92.

MCDONALD, J.
1960. The behavior of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. J. Fish. Res. Board Can. 17:655-676.

MCLAIN, D. R.
1968. Oceanographic surveys of Traitors Cove, Revillagigedo Island, Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 576, 15 p.

PARKER, R. R.
1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28:1503-1510.

ROBINSON, D. G., W. E. BARRACLOUGH, AND J. D. FULTON.
1968. Number, size composition, weight and food of larval

EFFECTS OF TRAP SELECTIVITY AND SOME POPULATION PARAMETERS ON SIZE COMPOSITION OF THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, CATCH ALONG THE MAINE COAST[1]

JAY S. KROUSE AND JAMES C. THOMAS

ABSTRACT

Information collected aboard commercial lobster boats along the Maine coast (1971-73) revealed, among other things, high numbers of sublegal lobsters (<81 mm carapace length) being handled by fishermen while sorting their catches. Throw-back ratios of illegal to legal lobsters (1.8 to 12.4:1) varied in association with lath spacing. Traps with spacings of $1\frac{5}{8}$ to $1\frac{3}{4}$ inches accounted for markedly fewer sublegals than those traps with $1\frac{1}{4}$- to $1\frac{1}{2}$-inch spacings.

Selectivity curves calculated for research traps with escape ports of $1\frac{1}{2}$, $1\frac{5}{8}$, and $1\frac{3}{4}$ inches and a trap escapement study demonstrate that a spacing of $1\frac{3}{4}$ inches is large enough to allow escapement of most sublegals yet small enough to retain legal lobsters. A regression of carapace length on carapace width shows that only an insignificant percentage of legal lobsters could physically squeeze through a $1\frac{3}{4}$-inch opening. Thus, results of this study led us to recommend that with a minimum legal length of 81 mm, traps should have $1\frac{3}{4}$-inch escape vents.

While riding aboard commercial lobster boats along the Maine coast (1971-73) to collect detailed catch and effort information, we frequently observed lobster fishermen sort and throw back from their traps excessive numbers of sublegal lobsters (<81 mm carapace length). When one considers that Maine lobstermen presently haul their traps more than 20 million times each year, the magnitude of this sorting becomes apprent. Lobstermen not only lessen the efficiency of their fishing operations by needlessly handling sublegal lobsters but they also inadvertently increase the lobsters chances of becoming a cull (missing claw[s]) or a victim to predatory fish while descending to the ocean floor (D. G. Wilder, pers. commun.), which in either case represents an economic loss to the industry.

A solution to this detrimental fishing practice became apparent to us after a cursory analysis of data from our earlier boat trips revealed an inverse relationship between lath spacing and numbers of sublegal lobsters. Templeman (1939) and Wilder (1945, 1948, 1954) also reported the same relationship based on size composition of catches from traps of various lath spacings. Although these Canadian scientists have long advocated the use of wider latch spacings to allow sublegals to escape, presently only Newfoundland has a lath spacing regulation of $1\frac{3}{4}$ inches.

Because of the management implications of this association between lath spacing and size composition of the catch, we undertook this investigation to quantitatively assess this situation with several independent approaches, namely: 1) selectivity curves; 2) trap escapement study; and 3) certain morphological dimensions of lobsters. Certain facets of this study were also valuable in corroborating some previously estimated population parameters such as natural mortality rates, sex ratios, and spawning stock structure and size.

These analyses have become increasingly important because we have recommended raising the legal minimum size from the present 81 mm ($3\frac{3}{16}$ inches) to 89 mm ($3\frac{1}{2}$ inches) carapace length. Then this study not only has application for the present situation, but also provides pertinent information for management of lobsters in the future.

METHODS

Samples from Commercial Gear

From 1971 through 1973, we spent 21 days riding aboard nine different commercial lobster boats (three boats were sampled more than once) from

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[1] This study was conducted in cooperation with the Department of Commerce, National Marine Fisheries Service, under Public Law 88-309, as amended, Commercial Fisheries Research and Development Act, Project 3-153-R.

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and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia May 1-4, 1967. Fish. Res. Board Can., Pac. Oceanogr. Group, Nanaimo, B.C., Manuscr. Rep. Ser. 964, 105 p.

SPARROW, R. A. H.
1968. A first report of chum salmon fry feeding in fresh water of British Columbia. J. Fish. Res. Board Can. 25:599-602.

WING, B. L., AND G. M. REID.
1972. Surface zooplankton from Auke Bay and vicinity, southeastern Alaska, August 1962 to January 1964. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Data Rep. 72, 765 p. on 12 microfiche.

four coastal areas. These boats were selected on a nonrandom basis because not all vessel-captains could or would accommodate us, nor could we reallocate committed time from our ongoing surveys of the natural lobster population and the commercial catch. While aboard these vessels we recorded the following: 1) numbers of sublegal and legal lobsters for each trap haul; 2) carapace length and sex of lobsters from a systematic sample of the catch, along with the corresponding measurements of lath spacings in these traps; 3) time expended in actual fishing as well as fishing time for each trap (number of set-over-days); 4) whether the fisherman was hauling one trap at a time (singles) or two attached traps with one buoy (pairs), or three or more attached traps (trawls) with two buoys, one at each end of the string; and 5) amount and kind of bait used.

Carapace lengths were measured in millimeters from the posterodorsal edge of the eye socket to the posterior margin of the carapace. In most cases, we attempted to measure all the lobsters in every *n*th trap (depended on whether traps were set as singles, pairs, or trawls); however, sometimes with two samplers, we were able to measure and record all the lobsters in each of the total number of traps hauled for the day.

Length compositions of the catches for each boat trip were used to calculate what we refer to as retention curves. These curves are simply an accumulative percentage of the number of lobsters by 1-mm carapace increments that were retained in the systematic sample of the traps hauled, along with measurements of the lath spacings of these traps. Because lath spacings were not uniform for each of the traps hauled per boat, the term "modal spacing" was used to imply that at least a majority of the traps per boat had a spacing more frequently measured by us than any other.

Samples from Research Gear

Since 1968 we have recorded the carapace length, weight, sex, condition (hard or soft shell, lost appendages) of individual lobsters caught in our research traps. Our research gear consisted of: 1) modified wooden traps, with plastic escape vents of 1½, 1⅝, and 1¾ inches (Figure 1), and 2) 1 × 1 inch wire meshed traps especially designed to catch sublegal lobsters. The modified commercial gear was fished from July 1972 through 1973, while the wire traps were used since 1968.

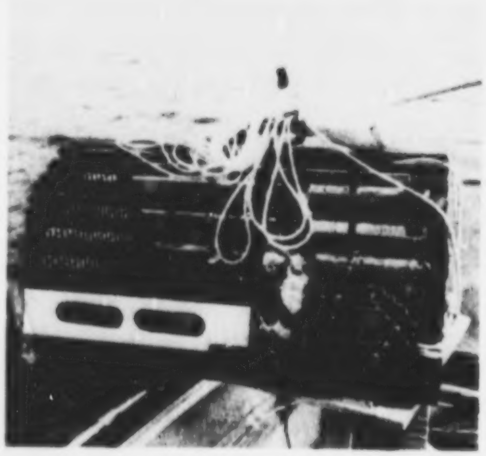

FIGURE 1.–Modified commercial lobster trap equipped with a plastic escape vent.

We also conducted a trap escapement study whereby lobsters of known sizes were placed in wooden traps with vents of 1¼, 1½, 1¾, and 2 inches. Because the heads or entrances were sealed, any escapement should have been accomplished between the laths. Through a 2-wk period traps were usually checked daily for escapement.

Comparison of Samples from Commercial and Research Gear

Following the methodologies of Beverton and Holt (1957), Pope (1966), and Gulland (1969), we calculated selectivity curves which were based upon carapace lengths of lobsters retained in the commercial gear with modal lath spacings of 1¼, 1⅝, and 1¾ inches. These data were proportioned with the same range of lengths retained in the 1 × 1 inch wire meshed research traps. Both sets of data, commercial and research, were weighted by trap-haul-set-over-days (THSOD). These comparisons were from the same general area, but not with the same groups of traps nor necessarily during the exact same period of time.

In addition, we used the cited methods to make selectivity determinations from the modified commercial traps that had specific lath spacings of 1½, 1⅝, and 1¾ inches. These spacings were proportioned with the data from the wire research traps (1 × 1 inch mesh). In this case, the modified commercial and wire research traps were fished simultaneously with the same spatial and temporal arrangements.

Body Proportions of Lobsters

To circumvent the spatial and temporal problems between commercial (boat trips) and research gear to a certain extent, we took body measurements of 217 lobsters, specifically carapace length, width, and height for sizes between 70 and 90 mm carapace length. These measurements should enable us to reach a more objective determination concerning the retention and escapement potential of various sized lobsters through different lath spacings.

RESULTS AND DISCUSSION

Samples from Commercial Gear

For the 21 boat trips with commercial fishermen, we counted their entire catch of 12,071 lobsters of which there were 2,311 legal lobsters (Table 1). This catch resulted from 4,026 trap hauls for a catch of 0.57 legal lobsters per trap haul or 0.22 legal lobsters per THSOD.

There are omissions in some of the data categories per boat trip because the sampling procedure evolved from successive trips aboard vessels; thus samplers learned by experience and observation what could or could not be accomplished under different physical conditions in each vessel. Nevertheless, subtotals can be gleaned from the boat trips with the more complete information. For example, there were 156 berried and/or "V"-notched females from 18 of the 21 boat trips. Even though this is a subtotal, it is an alarmingly low number. Of course, such things as season of year, area fished, and availability of berried females could affect this number. Still, we continue to be concerned about the possibility of a precarious limit of an adequate spawning stock (Thomas 1973; Krouse 1973).

The percent females is another estimate related to the reproduction potential of the exploited population of lobsters. For those lobsters that we measured and determined sex, 52.9% were females (sublegal and legal). This estimate is close to the 49.0 to 53.8% females that we estimated by year (1966-73) from the survey of the commercial (legal lobsters) and natural (mostly sublegal) population of lobsters.

These estimates are in conflict with the expectation that there should be more males than females in the commercial catch because berried and/or V-notched females must be returned to the ocean by law. Again, this situation points to a low number of sexually mature females.

To reach definite conclusions concerning the stock-progeny-recruitment relationships, we should follow the procedures of Beverton and Holt (1957) and Ricker (1958). This will be possible with continued support of this program and continued surveys on the commercial and natural populations of lobsters.

Length Frequencies

We measured the carapace length of 3,595 lobsters; the sex ratio (male:female) was 1:1.2. A histogram of these length frequencies (Figure 2) portrays the same situation that we have demonstrated from the commercial and natural surveys. That is, there are relatively large numbers of lobsters (2,937 or 81.7%) under the legal minimum size, while there are considerably fewer lobsters (658 or 18.3%) at and above the legal minimum size of 81 mm ($3^3/_{16}$ inches) carapace length. In fact, 94.0% of the legal catch is constrained within a ½-inch size range immediately above the legal minimum size. These conditions confirm the high exploitation rate of 0.86 that can be calculated from Thomas (1973).

Considering the modal lath spacings of traps used in each boat trip, there is a marked difference in the number of sublegal- and legal-sized lobsters.

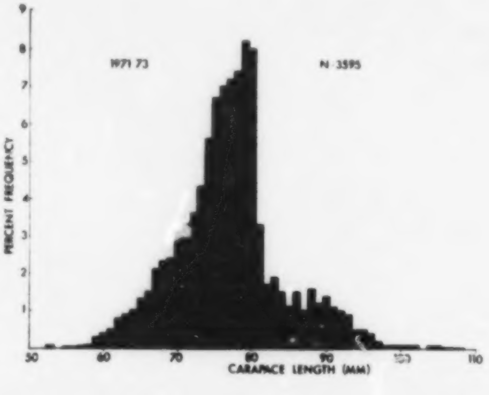

FIGURE 2.–Length-frequency distributions of lobsters caught in traps several lath spacings) used by commercial fishermen (1971-73).

TABLE 1.—Catch and effort statistics of 21 daily lobster catches for nine commercial fishing boats, September 1971 through September 1973.

	Catch, counted						Catch, measured		Catch-effort					Trap specifications		Bait	
			Females														
Area Boat trip (Date of trip)[1]	Total no.	Illegals: legal	Berried non V notch	Berried V notch	Non-berried V notch	Subtotal	Total no.	Females (%)	Legals per trap haul	Sublegals per trap haul	No. of trap hauls	No. of set-over-days	Boat hours	No. of parlors	Modal vent spacing (inches)	Amount (bu)	Type
Boothbay:																	
1. (Sept. 71)A	434	10.4:1	0	3	1	4	—	—	0.29	2.97	132	3	7.5	1	1.25	2	redfish
2. (Oct. 71)A	296	8.3:1	0	2	4	6	55	61.8	0.27	2.22	117	5	6.0	1	1.25	2	redfish
3. (Aug. 72)B	642	2.4:1	0	2	2	4	144	46.5	0.56	1.37	329	2	6.5	1	1.62	—	—
4. (Aug. 72)C	109	8.1:1	0	0	1	1	109	39.4	0.41	3.31	29	3	3.0	1	1.25	1	flatfish
5. (Aug. 72)B	696	2.6:1	0	3	3	6	134	57.5	0.62	1.81	310	—	6.5	1	1.62	5	redfish
6. (Sept. 72)A	428	12.4:1	0	3	0	3	204	52.0	0.13	1.58	248	3	7.3	1	1.25	2	redfish
7. (July 73)B	624	1.8:1	0	5	7	12	138	58.6	0.74	1.28	303	4	7.0	1	1.62	6	redfish and menhaden
8. (Aug. 73)B	637	2.9:1	0	2	25	27	128	50.8	0.85	1.79	250	2-4	8.0	1	1.62	4	redfish
9. (Sept. 73)A	340	8.7:1	0	0	6	6	245	57.6	0.27	2.32	129	5	7.0	1	1.25	2	redfish
Medomak:																	
10. (Sept. 71)D	1,247	5.6:1	0	3	12	15	—	—	0.76	4.18	249	3-4	12.5	1-2	—	6	redfish
11. (Nov. 71)D	1,606	3.5:1	4	3	9	16	347	([2])	1.34	4.62	267	6	11.0	1-2	—	6	redfish
12. (Sept. 72)D	1,234	4.5:1	3	6	8	17	280	57.7	0.96	4.22	235	4	12.0	1-2	1.25-1.50	6	redfish
13. (Sept. 73)D	926	3.6:1	0	4	12	16	58 145	([2]) 59.3	1.32	4.70	151	3	7.3	1-2	1.25-1.50	3	redfish
Jonesport:																	
14. (July 72)E	277	7.2:1	—	—	—	—	57	54.0	0.17	1.23	198	—	8.0	—	—	—	—
15. (Aug. 72)F	244	5.8:1	—	—	—	—	43	44.2	0.24	1.40	149	—	7.0	—	—	—	—
16. (Sept. 72)G	291	3.3:1	—	—	—	—	72	44.4	0.45	1.49	150	—	—	—	1.25	—	—
Newagen:																	
17. (Aug. 72)H	441	11.6:1	1	1	5	7	441	51.5	0.27	3.04	131	1-2	—	1	1.13-1.25	2	herring
18. (June 73)H	186	8.3:1	0	0	4	4	180	54.1	0.18	1.45	112	2-5	5.0	1	1.13-1.62	2	pollock
19. (July 73)H	329	4.9:1	0	5	1	6	327	51.7	0.43	2.05	130	1	5.0	1	1.13-1.62	1	herring
Cundy's:																	
20. (Sept. 72)I	554	9.7:1	0	0	4	4	232	54.7	0.30	2.91	171	2-3	7.3	1-2	1.75	4	redfish
21. (Sept. 73)I	528	3.2:1	0	2	0	2	280	51.4	0.53	1.69	236	2-3	7.3	1-2	1.75	4	redfish
Total	12,071	4.2:1	[3]8	[3]44	[3]104	[3]156	[3]3,595	[3]52.9	0.57	2.39	4,026	[3]1-6	[3]141.2	[3]1-2	[3]1.13-1.75	[3]58	

[1] Letters (A, B, etc.) represent boat trips with the same or different fishermen.
[2] Sex not determined.
[3] Data omissions.

For example, the catches of boat trips numbered 3, 5, 7, 8, 20, and 21 (modal lath spacings of 1⅝ or 1¾ inches) consisted of a low number of sublegal lobsters compared to the high number of sublegals in catches of boat trips numbered 2, 4, 6, 9, 17, 18, and 19 (modal lath spacings of 1¼ to 1½ inches) (Table 2).

TABLE 2.–Length-frequencies by 1-mm increments for lobsters collected in 21 commercial boat trips, September 1971 through September 1973 (successive boat-trip numbers are identical to those in Table 1).

Carapace length (mm)	Successive boat trips																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Totals
≤59	(1)	—	—	2	—	—	—	—	1	(1)	—	—	—	—	—	—	9	4	11	—	1	28
60		—	—	—	—	—	—	—	—		—	1	—	—	—	—	5	1	5	1	1	14
61		—	1	—	—	2	1	—	2		2	—	1	—	—	—	4	1	4	—	—	18
62		1	—	2	—	1	—	—	3		—	1	—	—	—	2	10	7	2	1	—	30
63		2	—	1	—	1	—	—	1		—	1	1	3	—	2	9	3	6	3	—	33
64		—	—	1	1	2	—	1	2		2	1	1	2	3	—	8	2	10	1	—	37
65		—	—	1	—	4	—	—	3		2	3	1	—	3	2	10	6	9	1	—	45
66		1	—	2	—	6	—	1	10		2	—	2	1	1	1	10	3	12	3	—	55
67		—	—	4	—	4	1	—	5		3	3	4	1	1	1	23	6	18	1	—	75
68		1	1	4	—	5	—	1	2		7	5	2	3	4	2	15	10	16	5	—	83
69		6	1	3	—	3	2	1	12		2	3	6	3	2	3	14	9	10	6	—	86
70		1	—	7	—	4	1	—	8		11	13	9	1	4	2	22	7	14	5	3	112
71		2	2	2	1	8	1	2	8		13	8	10	—	2	—	21	8	13	8	8	117
72		5	1	6	1	9	1	2	12		10	7	3	1	1	3	20	11	15	11	9	128
73		—	2	7	3	7	4	4	21		16	6	6	2	5	8	20	6	14	15	10	156
74		7	2	2	7	18	10	6	9		11	21	10	1	1	1	33	9	18	20	16	202
75		3	7	8	11	20	9	6	14		29	14	14	1	1	6	29	12	22	23	11	240
76		5	11	7	11	14	10	7	14		29	18	15	3	3	5	34	13	10	20	22	251
77		2	13	8	13	11	14	8	23		23	15	13	2	2	—	35	10	14	21	31	258
78		2	15	6	12	23	10	12	18		31	20	15	2	2	7	11	14	15	23	29	267
79		6	13	11	14	16	19	18	13		31	31	20	1	1	1	27	11	14	17	29	293
80		2	17	5	14	19	7	14	19		33	32	15	3	1	3	30	7	10	18	40	289
81		1	12	7	5	8	9	3	10		12	7	11	—	—	4	3	2	8	3	15	120
82		2	4	2	3	1	5	4	2		5	3	6	1	—	1	4	1	5	3	8	60
83		1	10	1	8	1	3	5	7		3	2	2	2	—	1	6	2	9	2	5	70
84		—	3	2	3	1	5	5	4		7	2	4	4	1	—	5	2	5	—	1	54
85		—	5	2	2	2	3	4	—		1	5	4	1	—	—	—	1	2	2	6	40
86		2	2	—	4	5	2	4	2		4	4	6	3	—	4	2	—	2	2	7	55
87		—	4	—	1	1	5	1	1		2	4	1	1	—	—	4	1	4	1	6	37
88		—	3	—	4	2	4	5	5		8	4	4	—	—	1	2	2	5	3	5	57
89		—	3	1	2	1	3	3	2		9	1	4	3	—	1	1	1	3	3	2	43
90		1	1	2	2	2	2	2	3		11	3	2	3	—	3	4	—	4	2	5	52
91		1	2	1	3	1	2	4	—		5	5	—	—	1	—	1	1	5	2	4	38
92		—	2	—	1	—	1	2	1		5	3	2	—	—	2	2	2	5	2	4	34
93		—	2	—	3	2	2	2	—		3	2	1	1	2	—	5	1	3	3	1	33
94		—	2	—	—	—	—	—	2		6	2	2	1	—	—	—	—	1	—	—	16
95		—	2	—	1	—	—	—	1		3	2	3	1	—	—	1	1	1	—	1	17
96		—	—	—	1	—	—	—	1		2	2	—	5	—	1	—	—	1	—	—	13
97		—	—	—	1	—	—	—	1		—	1	—	1	2	—	1	—	—	—	—	7
98		—	—	—	—	—	—	—	—		—	1	—	—	—	1	—	1	1	—	—	4
99		—	1	—	—	—	—	—	—		—	—	—	—	—	1	—	2	—	—	—	4
100		—	—	—	—	—	—	—	1		1	1	1	—	—	—	—	—	1	—	—	5
101		—	—	—	—	—	—	1	—		—	—	—	—	—	2	—	—	—	—	—	3
102		—	—	—	—	—	—	—	—		—	1	—	—	—	—	—	—	—	1	—	2
104		—	—	—	—	—	—	—	—		—	1	—	—	—	1	—	—	—	—	—	2
105		—	—	1	—	—	—	—	1		1	—	—	—	—	—	—	—	—	—	—	3
106		—	—	—	—	—	—	—	—		1	—	—	—	—	—	—	—	—	—	—	1
107		1	—	—	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	1
108		—	—	—	—	—	—	—	—		—	1	—	—	—	—	—	—	—	—	—	1
≥110		—	—	1	2	—	—	—	1		1	—	—	—	—	—	1	—	—	—	—	6
Totals		55	144	109	134	204	136	128	245		347	260	201	57	43	72	441	180	327	232	280	3,585

[1] No lengths taken.

Effects of Throw Backs on the Fishery

The throw-back ratios of illegal (sublegal plus berried and/or V-notched females) to legal lobsters which ranged from 1.8 to 12.4:1, confirmed our earlier observations that a considerable number of lobsters are being handled needlessly (Table 1). It is not difficult to envision sublegal, V-notched, or berried female lobsters spending a portion of their lives airborne. One of the important considerations in this situation is whether these lobsters suffer a higher natural mortality than those lobsters less than 51 mm (2 inches) carapace length which are seldom caught because of their possible secretive behavioral patterns and the selectivity of lobster traps. However, we might reach some tentative conclusions from the lengths of lobsters collected in the present study along with those from the commercial and natural surveys (Thomas 1973; Krouse 1973). The commercial survey shows that about 6% of the yearly catch are culls (one or both claws missing). Because most of the legal catch is recently recruited, this may indicate that frequent removal from traps of sublegal lobsters is, in part, responsible for this percentage of culls in the commercial catch. This could occur because the claws of those sublegals might grasp laths, knitted heads and parlor entrances, hands of fishermen, and the like. When such lobsters are pulled from the traps by fishermen, the claws are occasionally broken off. Another contributing factor might be that sublegal and legal lobsters sometimes extrude their claws through the lath spacings as the trap is hauled aboard the vessel. In this way, claws could be broken off. The design of the proposed "vented" trap, discussed later, takes this situation into consideration.

In order to evaluate more fully the possibility of a higher natural mortality due to handling, we used three independent approaches as follows:

1. Our observations aboard vessels show that the percentage of culls of sublegals is between 5 and 10%. This might indicate that natural mortality has not increased due to handling because of the similarity of the percentage of culls in the sublegal and legal size range of lobsters. Autotomy of the lobster could also confound the percentage of culls; however, we theorize that this particular percentage should not be different from the sublegal to legal sizes that we are studying.
2. Another insight on the effect of natural mortality would be the length frequencies of the sublegal lobsters caught by research gear in the sampling of the natural population (Figure 3), as well as the length frequencies from sampling aboard commercial vessels (Figure 2), although gear selectivity is a factor in this case. We should expect a higher mortality due to handling to show a significant decline in the number of sublegal lobsters as the size range increases by 1-mm increments from 70 (fully vulnerable size) to 81 mm (legal minimum size). Then the number of lobsters at, say, 80 mm should be less than those at 70 mm, not only due to the higher incidence of handling this larger size, but also because of the natural mortality that would occur without handling. These numbers at the specific sizes do not show this decline that could be attributed to a higher mortality due to increased handling (Figure 3).
3. As a supplement to the incidence of handling lobsters and the resultant natural mortality, we feel that our observations on the storage of lobsters in "pounds" (this procedure is described in Thomas 1973) might give information on the amount of natural mortality in the natural population and that mortality due to handling. The pound owners, stocking at the rate of one to two lobsters per square foot, tell us that a reduction of around 5% in numbers is normal for legal lobsters stocked to those reclaimed 3 to 5 mo later. Under these adverse conditions of crowding and handling in the pound as opposed to the situation in the natural environment, we infer that the annual natural mortality is low in the ocean (5 to 15%) and that handling has a minimal effect.

   The loss in lobster pounds is sometimes much higher than 5%, but in most of these situations the higher loss can be attributed to disease, adverse environmental conditions, and escapement.

Despite these speculative premises concerning the negligible effects of handling on natural mortality, the fishermen should still eliminate this needless sorting of large numbers of sublegal lobsters to reduce: 1) the time spend sorting sublegal from legal lobsters in traps, and 2) the eventual number of culls in the legal catch. Culls not only lessen the total poundage of the commercial catch but possibly the growth rate of culls may be slower than that of nonculls; Stewart and Squires (1968) suggest that molting of unduly stressed lobsters may be inhibited. The section on selectivity will demonstrate the potential benefit of proper lath spacing.

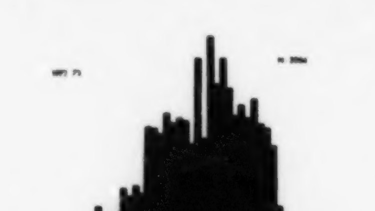

FIGURE 3.–Length-frequency distributions of lobsters collected with wire traps (1 × 1 inch mesh) at Boothbay Harbor (1972-73).

Retention Curves

The accumulative length frequencies by 1-mm increments from two selected boat trips reflect a characteristic sigmoid curve (Figure 4). Snedecor (1956) and others caution that although these curves are characteristic of normal distributions, other types of distributions could result in a sigmoid curve. For our purposes, we assume that these data represent normal distributions.

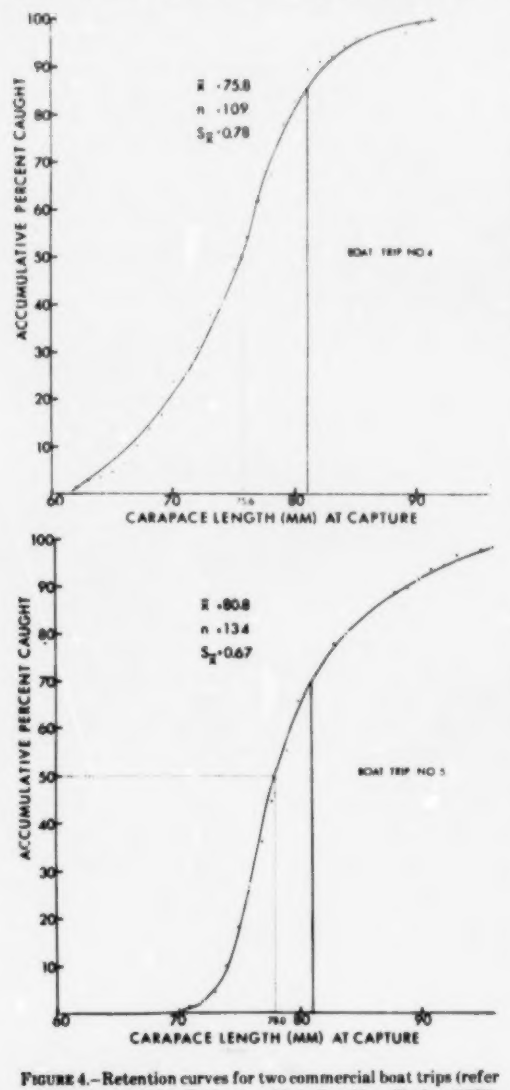

FIGURE 4.–Retention curves for two commercial boat trips (refer to boat trips 4 and 5 in Tables 1 and 2) in Boothbay Harbor (1972). Boat trips 4 and 5 had modal vent spacings of 1¼ and 1⅝ inches, respectively.

These curves are interesting in themselves because the 50% accumulative point demonstrates the influence of different lath spacings on the size, composition of the catch. For instance, boat trips 4 (1¼-inch vent) and 5 (1⅝-inch vent) had 50% accumulative points of 75.6 and 78.0 mm, respectively; thus demonstrating that traps with 1¼-inch vents are more selective for smaller lobsters (85% of catch ≤81 mm) than traps with 1⅝-inch vents (70% of catch ≤81 mm); while we are not advocating using these curves in place of selectivity curves, however we do suggest that these "retention curves" could be used as a quick, preliminary approximation of the influence of different lath spacings (gear selectivity) on the size composition of the catch in a trap fishery.

Selectivity Curves

Based upon the length composition of our catches with modified commercial traps equipped with escape ports (plastic vents) of 1½, 1⅝, and 1¾ inches and the 1 × 1 inch wire meshed traps, we calculated selectivity curves in accordance with the methodology of Beverton and Holt (1957). These catch data by 1-mm increments were weighted by THSOD and then the resultant values for each of the three vents (lath spaces) were proportioned with those of the wire traps over the same range of carapace lengths.

Traps with the same lath spacings had similar selectivity curves for the 1972 and 1973 catches while conspicuous differences are evident between the various size vents (Figure 5). In both years the 1½-inch vent was selective for the smaller sizes (50% retention ranged from 68.2 to 68.6 mm carapace length), the 1⅝-inch vent for the intermediate sizes (50% retention ranged from 71.4 to 73.5 mm carapace length), and the 1¾-inch vent for larger sizes (50% retention ranged from 75.4 to 78.8 mm carapace length). Contrary to most selectivity studies the important consideration in this study is not the mean selection length (50% point at which half the lobsters escape and half are retained); but rather, the proximity of the curve to the minimum legal size (81 mm carapace length) and whether or not the 100% retention point occurs below or above the minimum legal size. According

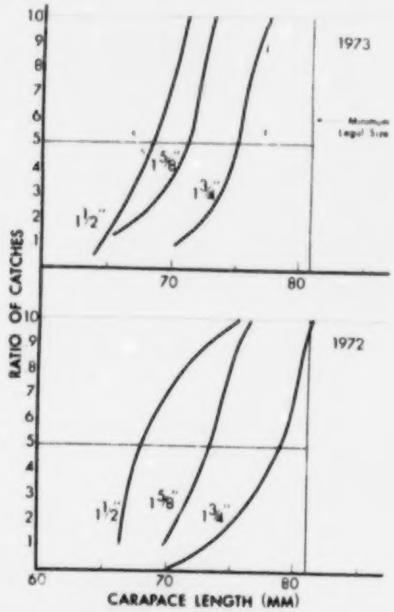

FIGURE 5.–Selectivity curves for each of the three vent sizes (1½, 1⅝, and 1¾ inches) of the modified commercial traps compared to wire (1 × 1 inch mesh) traps for 1972 and 1973.

to the selectivity curves, all three vents would prohibit the escapement of legal-sized lobsters. However, the 1¾-inch curve falls closer to the 81-mm line, thus demonstrating that this size vent allows a greater percentage of sublegal lobsters to escape than the 1⅝- or 1½-inch vents.

Effects of Vent Size on Trap Efficiency

Catches with modified commercial traps reveal an inverse relationship between vent size and the ratios of sublegal to legal lobsters (Table 3). Overall catches with traps having a 1¾-inch vent always consist of more legal than sublegal lobsters while this size composition is reversed in the catches from traps with smaller vents. This further substantiates our contention that excessive handling of short lobsters in the lobster fishery can be minimized with the addition of a 1¾-inch vent to all lobster traps.

TABLE 3.–Ratios of sublegal to legal lobsters captured with wire (1 × 1 inch mesh) and modified commercial (1½-, 1⅝-, and 1¾-inch vents) lobster traps, 1972 through 1973. Actual numbers of sublegal and legal lobsters appear in parentheses.

Year	Vent size (inches)			
	1 × 1 (wire)	1½	1⅝	1¾
1972	11.73:1 (962:82)	3.94:1 (71:18)	2.60:1 (78:30)	0.75:1 (21:28)
1973	28.09:1 (927:33)	5.86:1 (164:28)	1.44:1 (133:92)	0.76:1 (104:136)

Throughout this study, traps with 1⅝- and 1¾-inch vents not only retained fewer sublegal lobsters but seemed to capture proportionally more legal-sized lobsters than did those traps with 1½-inch vents. To assess this situation, we calculated separate catch-effort values (numbers of lobsters per THSOD) for legal-sized and all-sized lobsters combined for each of the three vent sizes (Figure 6). Indeed, our data indicate that traps with larger vents (1⅝ and 1¾ inches) are more successful in retaining greater numbers of legal lobsters than traps with smaller vents. However, because of our limited field sampling, we cannot validly conclude that this disparity in efficiency between vents is conclusive evidence, but rather that our data strongly suggest this possibility.

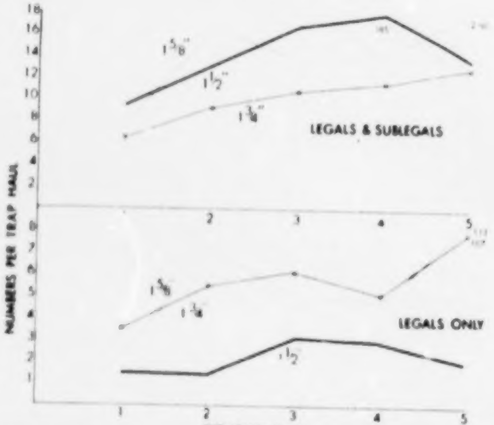

FIGURE 6.–Comparisons of the number of lobsters (legals, sublegals, and legals combined) per trap-haul-set-over-day for modified commercial traps with vents of 1½, 1⅝, and 1¾ inches (1972-73).

Body Proportions of Lobsters

The escapement of lobsters of given sizes from traps with varying lath spacings depends upon certain morphological dimensions such as carapace length, width, and height. We contend that the width of the carapace is more important than the height because we observed in the laboratory that lobsters, attempting to escape through different lath spacings, would twist on their sides when encountering a tight fit between laths. This, coupled with the fact that the width is always smaller than the height for any carapace length, led us to the opinion that the relationship between carapace length and width in association with lath spacing is the important consideration for gear selectivity studies. We calculated the regression of carapace length (X) on width (Y) for 217 lobsters (114 females and 103 males) by the method of least squares. The calculated equation was $Y = -4.367 + 0.649X$ (Figure 7). Data for sexes were combined because analysis of covariance on the regression coefficients (Steel and Torrie 1960) showed that carapace length-width ratios of males and females did not differ significantly.

According to this relationship, lobsters at the minimum legal size of 81 mm carapace length would be expected to have a mean carapace width of 48.2 mm + 0.18 with individual widths within the 95% prediction interval ranging from 45.6 to 50.9 mm. The magnitude of these measurements relative to a 1¾-inch (44.5-mm) lath spacing suggests that only a very small percentage of legal-sized lobsters might escape through that size vent.

We should mention that some compression of the shell, particularly if the lobster is newly molted, is possible as a lobster struggles to get through the lath spacing of a trap. However, based upon our laboratory observations, we would not expect this compression to exceed 2 to 3 mm for soft-shelled lobsters (1 to 2 wk since ecdysis) and 1 mm for a hard-shelled lobster. Because this soft-shelled condition is of rather brief duration and the frequency of trap hauls is greatest during the shedding season (a shorter period of time for escapement), these situations should minimize escapement.

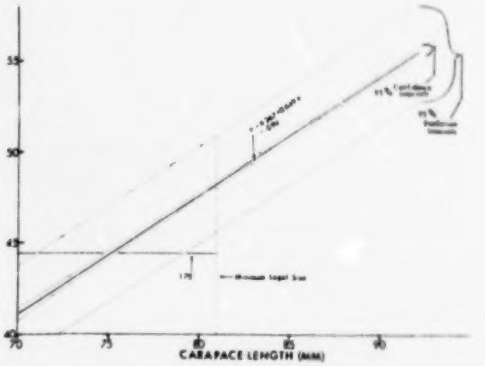

Figure 7.–Carapace length-width relationship for lobsters with 95% confidence and prediction intervals.

Trap Escapement Study

Retention curves, based on the escapement of lobsters of known lengths from traps with lath spacings ranging from 1¼ to 2 inches, graphically display the pronounced effect escape vent size has on lobster escapement (Figure 8). Retention of sublegal lobsters was high for the 1¼- and 1½-inch traps while most sublegals were able to escape from traps with the 1¾- and 2-inch vents. With the present minimum size of 81 mm (3³/16 inches), a 2-inch vent would be unsatisfactory as many legal lobsters could escape, whereas escapement of legals through a 1¾-inch vent would be extremely minimal. Although the curve for the 1¾-inch vent did show some escapement, we believe this escapement is exaggerated by the methodology (plotting midpoints) employed in the derivation of this curve. This contention is further substantiated by the fact that only one of seven lobsters with a carapace length of 82 mm escaped and there was no escapement for lobsters larger than 82 mm.

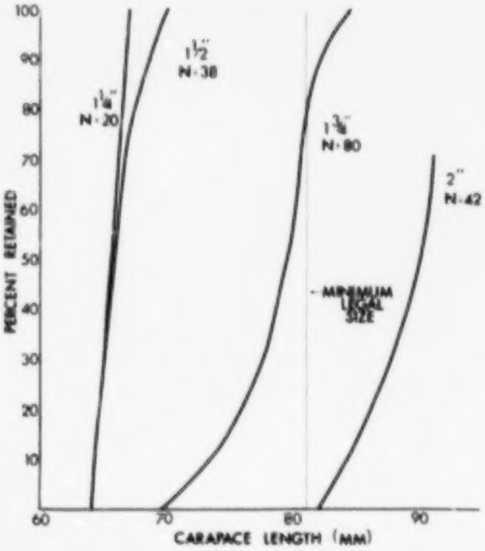

Figure 8.–Retention curves for lobsters placed in modified commercial traps with 1¼-, 1½-, and 1¾-, and 2-inch vent dimensions.

RECOMMENDATIONS

Based on the foregoing analysis of the effects different lath spacings have on the size composition of lobster catches, we recommend that all lobster traps fished along the Maine coast have an escape vent of 1¾ inches. Of course, if the minimum legal size (81 mm) is increased then the vent size should be altered accordingly.

We emphasize that it is not necessary for the entire trap to consist of the desired lath spacing; but rather, only one lath spacing either on the side or end (preferably near the bottom) of the parlor section of the trap. The remaining laths could be spaced at the fisherman's discretion.

We believe an escape port (vent) fabricated from some type of durable material and manufactured to our specifications could be incorporated into any conventional lobster trap (Figure 1). Merits of this vent would be: 1) easy installation in both new and old traps without requiring drastic modification; 2) modest cost to the fishermen; and 3) retention of its original dimensions over time (unlike wooden laths which eventually wear, causing a larger opening, thus permitting escapement of legal lobsters).

If this recommendation of venting traps is adopted as a conservation measure, we would expect reductions in: 1) the number of culls (which in turn would increase the weight of the total landings) and, if of consequence, the natural mortality; 2) time expended by lobstermen in sorting their catches; 3) perhaps the illicit trade of sublegal lobsters (shorts) which is considered by some dealers and fishermen to be of an alarming magnitude; and 4) if a real problem, the number of lobsters imprisoned in lost traps.

ACKNOWLEDGMENTS

We thank the fishermen who allowed us, often at inconvenience to themselves, to accompany them on their fishing trips. Cecil Pierce, a fisherman from Southport, Maine, designed the plastic vent. Gary Robinson, Louis Kazimer, Curt Crosby, Andrew Dolloff, and William Sheldon of the Maine Extension Service made many of these trips. Their comments and experience aided greatly in collecting meaningful data. We express gratitude to Gareth Coffin, formerly with the Northeast Fisheries Center, National Marine Fisheries Service, West Boothbay Harbor, Maine, for his photographic work.

LITERATURE CITED

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric., Fish. Food (G. B.), Ser. II, 19, 533 p.

GULLAND, J. A.
1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO (Food Agric. Organ. U.N.) Man. Fish. Sci. 4, 154 p.

KROUSE, J. S.
1973. Maturity, sex ratio, and size composition of the natural population of American lobster, *Homarus americanus*, along the Maine coast. Fish. Bull., U.S. 71:165-173.

POPE, J. A.
1966. Manual of methods for fish stock assessment. Part III. Selectivity of fishing gear. FAO (Food Agric. Organ. U.N.) Fish. Tech. Pap. 41, 41 p.

RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.

SNEDECOR, G. W.
1956. Statistical methods applied to experiments in agriculture and biology. 5th ed. Iowa State Coll. Press, Ames, 534 p.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill, N.Y., 481 p.

STEWART, J. E., AND H. J. SQUIRES.
1968. Adverse conditions as inhibitors of ecdysis in the lobster *Homarus americanus*. J. Fish. Res. Board Can. 25:1763-1774.

TEMPLEMAN, W.
1939. Investigations into the life history of the lobster (*Homarus americanus*) on the west coast of Newfoundland, 1938. Newfoundland Dep. Nat. Resour., Res. Bull. (Fish.) 7, 52 p.

THOMAS, J. C.
1973. An analysis of the commercial lobster (*Homarus americanus*) fishery along the coast of Maine, August 1966 through December 1970. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-667, 57 p.

WILDER, D. G.
1945. Wider lath spaces protect short lobsters. Fish. Res. Board Can., Atl. Biol. Stn. Circ. G-4, 1 p.
1948. The protection of short lobsters in market lobster area. Fish. Res. Board Can., Atl. Biol. Stn. Circ. G-11, 1 p.
1954. The lobster fishery of the southern Gulf of St. Lawrence. Fish. Res. Board Can., Gen. Ser. Circ. 24, 16 p.

EXPERIMENTAL EXPLOITATION OF COMPETING FISH POPULATIONS

RALPH P. SILLIMAN[1]

ABSTRACT

Populations of the guppy, *Poecilia reticulata*, and the swordtail, *Xiphophorus maculatus* × *X. helleri*, were grown both independently and in competition under controlled conditions. Independent populations were permitted to grow for about a year and then successively exploited at two different rates for each species. In the control (unfished) pair of competing populations, both species grew for about 30 weeks, followed by decline and extinction of the swordtail and fluctuations in the guppy. Similar initial growth in the test pair was followed by exploitation of both species at various combinations of rates.

Measures of recruitment were available as weights of juveniles returned to adult tanks from separate nursery tanks. Data from fitted curves showed that guppy recruitment exceeded that of the swordtail under both independent and competing conditions. Depression of recruitment by competition was greater in the swordtail than in the guppy.

A mathematical model for competing populations consisted of a pair of differential equations including elements of the Volterra competition formulae and the Fox exponential surplus-yield model. By using the exploitation rates applied in the experiments, and constants from the independent populations, the model was applied to biomass data from the control pair of competing populations. Successive trials resulted in a reasonably good fit, and competition coefficients from this were used to fit data from the exploited test pair. Yield isopleths calculated from the fitted model showed that maximal yields were obtained when exploitation for the swordtail was lower than for the guppy, suggesting lower productivity in the swordtail. The maximum sustainable yield represented about 20% of food placed in tanks, and indicated at least as great efficiency from competing populations as from independent ones.

Results from the experiments clearly suggest that exploiting both members of a competing pair is preferable to exploiting either alone, provided fishing rates are adjusted in relation to the productivity of each species.

Classical studies of fishery dynamics, such as those discussed in the works of Beverton and Holt (1957) and Ricker (1958), deal mostly with single populations treated as if they existed independently. Fishery biologists have come to recognize, however, that in many situations the fish stock cannot be so treated (Larkin 1963; Murphy 1973). The exploited population of interest is interdependent with others (which may be either exploited or unexploited) through competitive or predator-prey relations. Any effect of exploitation on one stock may produce a reaction in another, resulting in readjustments in both populations, and invalidating the expected response to exploitation based on single-species dynamics.

A familiar example of an apparent competitive situation is contained in the population histories of the Pacific sardine, *Sardinops sagax*, and the northern anchovy, *Engraulis mordax*, off the coast of California. The sardine suffered a catastrophic decline in the mid-1940's, followed by an increase in the anchovy. An analog computer model of Silliman (1969a, b) demonstrated that at least part of the change in the anchovy population size could be simulated with data on the sardine population size and the differential equations of Volterra (1928). Murphy (1973) provided recent verification of the sardine-anchovy relation and suggested that similar relations may prevail in the Japanese and South African sardines.

Laboratory experiments on the exploitation of self-sustaining fish populations have been reported fairly extensively (Silliman and Gutsell 1958; Silliman 1968; Nagoshi et al. 1972). Experiments with competing populations have included such diverse organisms as yeast cells (Gause 1932); Protozoa (Gause 1934); *Daphnia* (Frank 1957); beetles (Park 1962); and warblers (MacArthur 1958). To the best of my knowledge, however, exploitation of competing laboratory fish populations has not previously been reported.

The purpose of the experiments reported below was to ascertain experimentally the reaction of two competing fish populations to exploitation.

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Within this general objective, it was desired to determine which combination of exploitation rates applied on the two species would provide the maximum sustainable yield. To approach this problem, test and control pairs of populations were established in aquariums and allowed to grow several months under controlled conditions. Various combinations of exploitation rates were then applied to the test pair to determine population interactions and total yields. A "base line" for evaluating the results was obtained by growing and exploiting each of the competing species independently.

APPARATUS AND PROCEDURES

Experimental Animals

A lengthy fund of experience (Silliman 1948, 1968; Silliman and Gutsell 1958) built up with the guppy, *Poecilia reticulata*, dictated this as one of the experimental fishes. For the other, it was desired to have a species that was similar to the guppy in size, reproduction, and feeding habit but readily distinguishable from it in a mixed population.

A fish that met these requirements fairly well was the red swordtail hybrid, *Xiphophorus maculatus* × *X. helleri*, which will be referred to simply as "swordtail." It is somewhat larger than the guppy, but lived in the same sized aquarium. It is a live-bearer, like the guppy, and will readily eat the foods commonly fed guppies. Its brilliant red color permits easy distinction in the adults, and even the newborn young are pink or orange and may be distinguished from newborn guppies. In both species, adult males can be distinguished from adult females by external inspection. Distinguishing male characters are the modified anal fin (gonopodium) and fin and body color in the guppy and the elongated lower caudal fin ("sword") in the swordtail.

Aquarium Tanks

Fish were grown in four conventional glass-walled aquariums, each with a water surface of 44 cm by 24 cm, a water depth of 19 cm, and a volume of 20 liters. Inside each tank was an air-stone and a fiber-charcoal filter. Tanks were placed in a row with their longer axes parallel, and lettered A, B, C, D from left to right.

Tanks A and C were for juvenile and adult fish together. They each had a refuge in the left front corner for the escape and subsequent removal of recently born fish, or "fry." This refuge was formed with a fence consisting of 21 cm by 3 mm glass rods placed 1.5 mm apart, enclosing a right isosceles triangular space of 15 cm hypotenuse.

Although guppies could survive and achieve population growth in the above-described tanks, preliminary experiments showed this not to be true for the swordtails. Tanks B and D were therefore provided as "nurseries" for the temporary relocation of newborn young from tanks A and C, respectively. The juveniles were placed back in tanks A and C when they had grown to such size that they would no longer pass through a sieve consisting of 3-mm plastic rods placed 2 mm apart, thus making them recruits to the fishable stock.

Food and Feeding

A diet previously developed for guppies (Silliman 1968) was fed to all fish (Table 1). The food *Artemia* nauplii, however, requires special mention. The original intention was to feed the fish in the nursery tanks one-half the amount fed those in the adult tanks. The weight of nauplii produced was mistakenly believed to be directly proportional to amount of *Artemia* eggs placed in the culture beakers and, therefore, one-half the amount of eggs placed in the beakers for the adult tanks was placed in those for the nursery tanks. Production tests (Table 2) based on duplicate hatchings produced under standard conditions, however, showed production not to be proportional to the amount of eggs. Amounts of eggs inserted were kept the same, nevertheless, on the chance that unhatched eggs were eaten (observed on one occasion).

Artemia nauplii provided so small a proportion (1/100%) of the total diet that the lack of proportion noted above would have no significant effect on total food intake. The small amount of living food provided by the nauplii was regarded in the same sense as vitamins in human nutrition: as something required in small amounts for good health, but not furnishing a significant proportion of total food intake by weight. It is pertinent to note that the smallest number of nauplii (1,500) indicated by any of the tests (Table 2) would provide over four nauplii per fish for the largest

TABLE 1.—Food placed in tanks, grams.

Dates included	3-wk periods	Day of week	Adult tanks: Dry[1]	Adult tanks: Frozen *Artemia*	Adult tanks: *Artemia* nauplii	Adult tanks: Total	Nursery tanks: Dry[1]	Nursery tanks: Frozen *Artemia*	Nursery tanks: *Artemia* nauplii	Nursery tanks: Total
25 Oct. 1965 to 6 Dec. 1969	0-71	Sun.	0.1	—	—	0.1	0.05	—	—	0.05
		Mon.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Tues.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Wed.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Thurs.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Fri.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Sat.	0.1	—	(2)	0.1	0.05	—	(2)	0.05
		Total	0.7	5.0	—	5.7	0.35	2.5	—	2.85
7 Dec. 1969 to 1 Jan. 1973	71-124	Sun.	0.1	—	—	0.1	0.05	—	—	0.05
		Mon.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Tues.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Wed.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Thurs.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Fri. A.M.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Fri. P.M.[3]	0.1	—	(2)	0.1	0.05	—	(2)	0.05
		Total	0.7	5.0	—	5.7	0.35	2.5	—	2.85

[1] Tropical fish food.

[2] Hatch from 0.4 g (adult) or 0.2 g (nursery) of eggs (Table 2). Silliman and Gutsell (1958) found that the hatch from 0.4 g of eggs weighed 0.125 mg. Test hatches of nauplii were not proportional in weight to the amount of eggs used (Table 2), and since the total weight would be only 1/100% of the diet, no weight is indicated in the table.

[3] This was combined with the Friday A.M. feeding in 35 out of 161 wk and with the Sunday feeding once.

TABLE 2.—*Artemia* production tests. All 48-h hatches at 24°C in 800 ml 3% salt water. Counts from 20 samples for each test. Samples were 0.3 ml, withdrawn by pipette from vigorously stirred cultures killed in 0.75% formaldehyde, and replaced.

Test dates	Source of eggs[1]	Wt of eggs (g)	Mean no. in samples: Nauplii	Mean no. in samples: Eggs[3]	Est. 1,000s in culture[2]: Nauplii	Est. 1,000s in culture[2]: Eggs[3]
1970:						
1/28-30	A	0.2	2.10	7.50	5.6	20.0
1/28-30	A	0.4	1.45	18.05	3.9	48.1
3/23-25	A	0.2	1.85	6.95	4.9	18.5
3/23-25	A	0.4	2.05	16.30	5.5	43.5
4/13-15	B	0.2	1.75	10.35	4.7	27.6
1971:						
5/ 3- 5	B	0.4	0.55	32.95	1.5	87.9
5/17-19	B	0.2	0.85	23.30	2.3	62.1
5/24-26	C	0.2	3.50	30.70	9.3	81.9
10/ 4- 6	C	0.2	3.65	33.40	9.7	89.1
11/29-12/1	C	0.2	2.75	34.30	7.3	91.5
1972:						
5/15-17	C	0.2	6.85	27.80	18.3	74.1
11/13-15	C	0.2	2.75	36.10	7.3	96.3

[1] All were commercial suppliers.

[2] Sample numbers times 800/0.3.

[3] Includes shells (from hatched eggs) and unhatched eggs.

number of fish recorded in any tank (343 guppies in tank C during the last week of 3-wk period 65).

Dry food was placed on the surface of the water and sank slowly if not eaten immediately (as occurred with large populations). Frozen food sank and was eaten as it thawed. *Artemia* nauplii were hatched in 800-ml glass beakers (Table 2). The entire water mass, including shells and unhatched eggs, was poured through a cloth filter which was rinsed with freshwater and then rinsed into the fish tanks.

Cleaning and Treatment

Detritus including uneaten food (none in large populations) was siphoned daily from the tanks onto a cloth filter and the siphoned water returned to the tanks. Once a week all the water was removed from the tanks and one-half the volume was replaced with tap water aged for 1 wk. At this time the tanks and their equipment were thoroughly cleaned, and the filter fiber and charcoal were replaced. Also, fish in the adult tanks were treated for 15 min in a 1:200 solution of a commercial aquarium disinfectant "Fungistop."[2]

Water Characteristics

Water temperature in tanks A and D (Tables 3, 4; Figure 1) was recorded daily (Saturday excluded during 3-wk periods 71-124). These end tanks were chosen to reveal any temperature gradient that might exist. Although there was a slight tendency for tank D to vary from tank A (Figure 1), the differences were mostly less than 1°C and are not believed to have significantly affected population growth. It will be shown in the section on oscillatory fluctuation that deviations of population size from the theoretical were not correlated with tank temperature.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3.–Mean temperatures, °C, 3-wk periods, competing populations. Daily readings (21) to period 70, Sunday to Friday (18) from period[1] 72 on.

	Tank			Tank	
Period	A	D	Period	A	D
0	[2]24.2	[2]24.6	38	23.6	23.9
1	24.5	24.6	39	23.6	24.2
2	24.9	24.7	40	23.9	24.4
3	24.6	24.5	41	23.5	23.8
4	24.7	24.5	42	23.3	23.5
5	24.6	24.6	43	24.1	24.4
6	24.5	24.6	44	24.5	24.7
7	24.7	24.8	45	24.1	24.7
8	24.5	24.8	46	24.9	25.2
9	24.4	24.6	47	24.9	25.1
10	24.4	24.7	48	24.3	23.5
11	24.6	24.8	49	24.8	24.9
12	25.6	25.6	50	24.1	24.3
13	25.9	25.9	51	24.1	24.4
14	26.4	26.0	52	23.7	23.9
15	25.6	25.7	53	23.7	23.8
16	25.5	25.4	54	23.5	23.6
17	25.0	25.1	55	23.4	23.9
18	25.0	24.8	56	23.7	23.9
19	25.6	25.1	57	23.9	23.8
20	26.4	25.1	58	23.6	23.6
21	26.2	24.9	59	23.5	23.7
22	26.0	25.5	60	23.2	23.5
23	25.9	24.6	61	24.3	24.5
24	25.2	24.5	62	24.5	24.5
25	25.6	24.6	63	24.9	24.9
26	26.0	25.0	64	24.7	24.9
27	25.7	25.2	65	23.8	23.8
28	26.4	25.8	66	23.9	23.8
29	26.2	25.9	67	24.4	24.3
30	26.3	25.8	68	21.5	21.4
31	25.9	26.0	69	24.0	24.0
32	24.5	25.1	70	24.0	23.8
33	23.8	24.5	71	[1]23.9	[1]23.8
34	23.1	23.8	72	23.7	23.4
35	23.7	23.6	73	23.8	23.5
36	23.4	23.8	74	23.9	23.5
37	23.7	23.8	75	23.9	23.5

[1] One Friday and two Saturday readings missing, period 71.

[2] Based on 1 wk only.

TABLE 4.–Mean temperatures, °C, 3-wk periods, independent populations. Sunday to Friday readings (18).

	Tank			Tank	
Period	A	D	Period	A	D
79	24.6	24.1	102	24.5	24.3
80	23.5	23.2	103	24.7	24.2
81	25.0	24.5	104	24.5	23.6
82	24.7	24.3	105	24.4	23.6
83	24.4	24.2	106	24.3	23.5
84	24.5	24.5	107	24.1	23.8
85	24.3	24.3	108	24.2	23.8
86	23.9	23.7	109	24.3	23.9
87	24.2	23.8	110	24.4	23.9
88	24.2	23.6	111	24.3	23.8
89	24.6	23.9	112	24.5	23.9
90	24.6	23.9	113	24.6	23.9
91	24.6	24.2	114	24.6	23.9
92	24.5	23.8	115	24.1	23.5
93	24.5	23.9	116	25.8	25.2
94	24.6	23.7	117	25.6	24.9
95	24.2	24.0	118	25.4	24.7
96	24.3	23.9	119	24.9	24.1
97	24.2	23.6	120	24.5	23.6
98	24.4	24.2	121	24.7	23.6
99	25.6	25.4	122	24.1	22.9
100	25.7	25.4	123	24.5	23.3
101	24.7	24.5	124	[1]24.7	[1]24.2

[1] Last three readings missing.

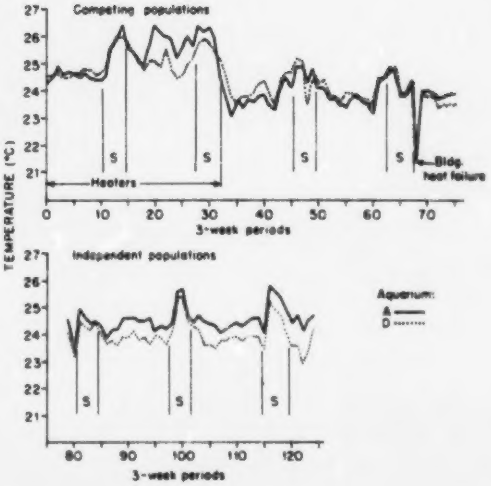

FIGURE 1.–Water temperatures (3-wk means). "S" indicates summer periods (approximately 20 June to 20 September).

Heaters were placed in tanks during periods 1-32 (Figure 1) but caused excessive temperature fluctuation and one instance of mortality from a nonfunctioning thermostat. During periods 33-174 the tank water was at room temperature. This was thermostatically controlled except that no cooling was available in the summer. Summer temperatures were thus somewhat higher than during the balance of the year (Figure 1), but the change was the same for all tanks.

Measurements of dissolved oxygen and carbon dioxide concentrations and pH were made at irregular intervals during the course of the experiment (Table 5). All O_2 readings were within or above the 3-5 ppm range considered satisfactory for warmwater fishes by Lewis (1963), and the CO_2 and pH readings were within the range he considered safe (CO_2<30 ppm., pH 5.0-9.0).

Light was provided from overhead fluorescent fixtures with standard tubes to period 11. After period 11, pink tinted tubes were used.

Handling, Enumeration, Exploitation, and Weighing

Areas behind the refuge fences described under "Aquarium Tanks" were inspected daily. If any newborn fish were found there or in other corners of the tanks, they were removed by netting or siphoning, counted, and placed in the nursery

TABLE 5.–Water condition on selected dates.

Dates		3-wk period	O₂, ppm.		CO₂, ppm.		pH	
			Tank A	Tank D	Tank A	Tank D	Tank A	Tank D
1968:								
Aug.	9	45	7.0	7.0	—	—	—	—
	16	48	6.0	—	—	—	—	—
	29	49	6.6	6.4	10	10	6.9	6.9
Sept.	6	49	6.2	6.8	—	—	—	—
	13	49	6.2	6.4	—	—	—	—
	20	50	6.4	6.4	10	10	—	—
	27	50	6.4	6.4	—	—	—	—
Oct.	4	50	6.4	6.4	—	—	—	—
	11	51	6.0	6.4	—	—	—	—
	18	51	6.4	6.8	—	—	—	—
	25	51	6.2	6.4	—	—	—	—
Nov.	8	52	6.0	6.6	—	—	—	—
	15	52	6.4	7.2	—	—	—	—
	28	53	6.4	7.0	—	—	—	—
Dec.	6	53	6.4	6.8	—	—	—	—
	13	54	6.4	6.6	—	—	—	—
	26	54	6.4	6.8	—	—	—	—
1969:								
Jan.	2	55	6.4	7.0	—	—	—	—
Sept.	17	67	6.6	6.6	10	10	8.0	8.0
Oct.	2	68	7.8	7.8	—	—	—	—
	9	68	7.4	8.2	—	—	—	—
	23	69	6.6	7.6	—	—	—	—
	30	69	6.2	7.6	—	—	—	—
Dec.	4	71	6.8	7.4	10	10	8.0	8.7
1971:								
Feb.	25-26	92	6.6	8.2	10	10	8.0	8.0
1972:								
Mar.	23	111	5.0	7.2	10	10	8.5	8.0

tanks. At the time of weekly cleaning, the water in the nursery tanks was poured through the sieve also described under Aquarium Tanks. Any fish remaining on the sieve were placed back in the adult tanks.

Fish were counted and weighed weekly during periods 0-71. During periods 71-124, this was done only at the approximate brood intervals of the fish, which were 3 wk for the guppy and 4 wk for the swordtail. Fish were counted simply by netting them from one container to another. Counts were categorized into "immature" (those whose sex could not be determined from external inspection), male, and female. Fry and juveniles were counted when moved between adult and nursery tanks. Dead fish found in tanks were recorded as mortalities.

Exploitation was done at the time of counting. To apply an exploitation rate of $1/n$, each nth fish was removed (n was always an integer). This was applied equally to juveniles and adults, but not at all to fish in the nursery tanks.

Population and catch weights were also determined at the time of counting. Fish were drained and placed in a previously weighed container of water. Total weight was measured and fish weight obtained by subtracting the tare.

COURSE OF POPULATIONS

Independent Populations

Although chronologically the competing populations preceded the independent populations, the more logical order of presentation is to deal with the independent populations first. This arrangement will be followed in the remainder of the report.

Separate populations of guppies and swordtails were started on 19 May 1970 (3-wk period No. 79). Each of these was permitted to grow for an initial period of about 1 yr (Figures 2, 3) before exploitation was begun. Even though complete equilibrium had not been reached, exploitation was started at 25% per brood interval (3 wk) for the guppy and 10% per interval (4 wk) for the swordtail. The lower rate for the swordtail was based on previous experience showing lower productivity for that species. Initial rates were maintained during weeks 289-334 for the guppy and 290-334 for the swordtail. Final rates were 33.3% for the guppy (weeks 337-373) and 16.7% for the swordtail (weeks 338-374). Responses were in accord with expectations for the guppy (Figure 2) and the early swordtail history, but there was an increase in both number and weight in the swordtail in the last five brood intervals (Figure 3). This anomaly will be discussed under "Oscillatory Fluctuation."

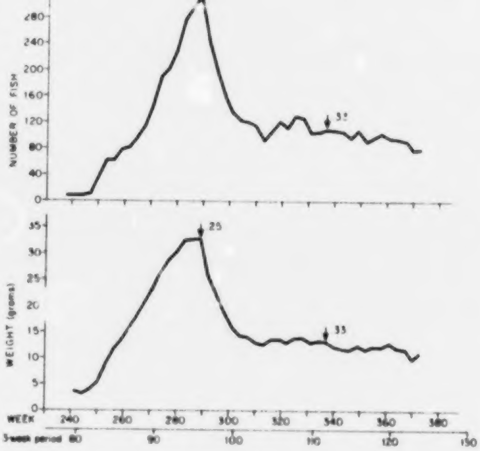

FIGURE 2.–Course of independent guppy population. Numbers indicate target exploitation rates.

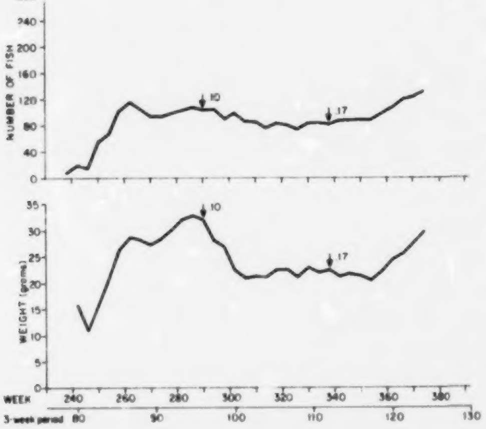

Figure 3.—Course of independent swordtail population. Numbers indicate target exploitation rates.

Competing Populations

The two mixed populations, each composed of both guppies and swordtails, were started 24 October 1965 (week 0). Three-week period 0 started with week 1, since weights were not recorded in week 0.

In the control (unexploited) pair of populations (Figure 4), both species grew for an initial period of about 30 wk. The swordtail population then began to decline and disappeared at week 129. This will be discussed in the section on competitive exclusion. Extinction of the swordtail was followed by a large oscillatory fluctuation in the guppy (about -39% to +26% of the asymptotic level), which will be discussed in the section on such fluctuations.

Initial growth in the test (exploited) pair was similar to that in the control pair (Figures 4, 5). Exploitation was started first on the swordtail

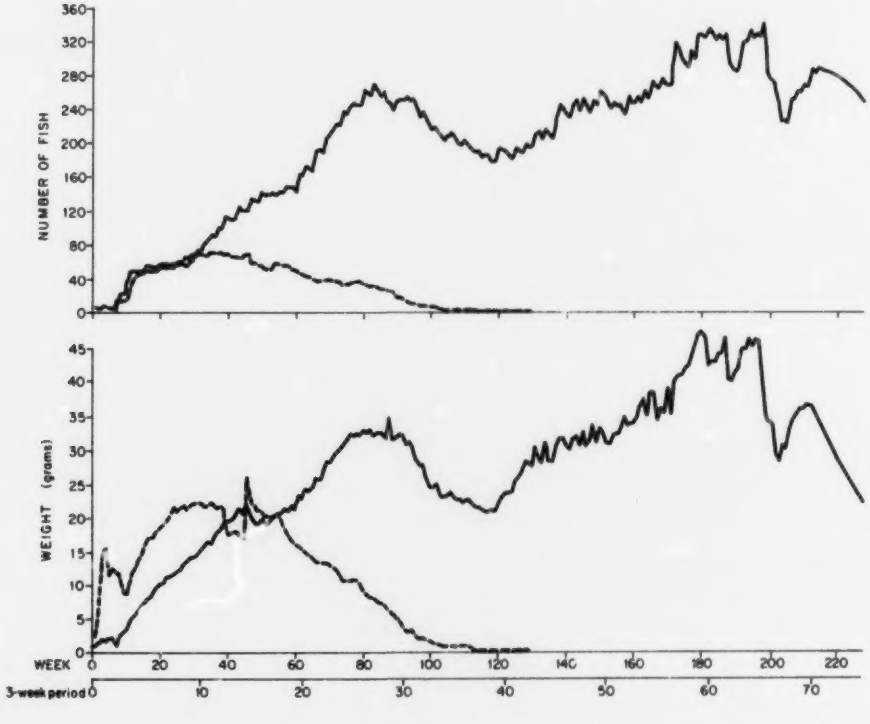

Figure 4.—Course of competing populations, control pair. Solid line, guppy; broken line, swordtail.

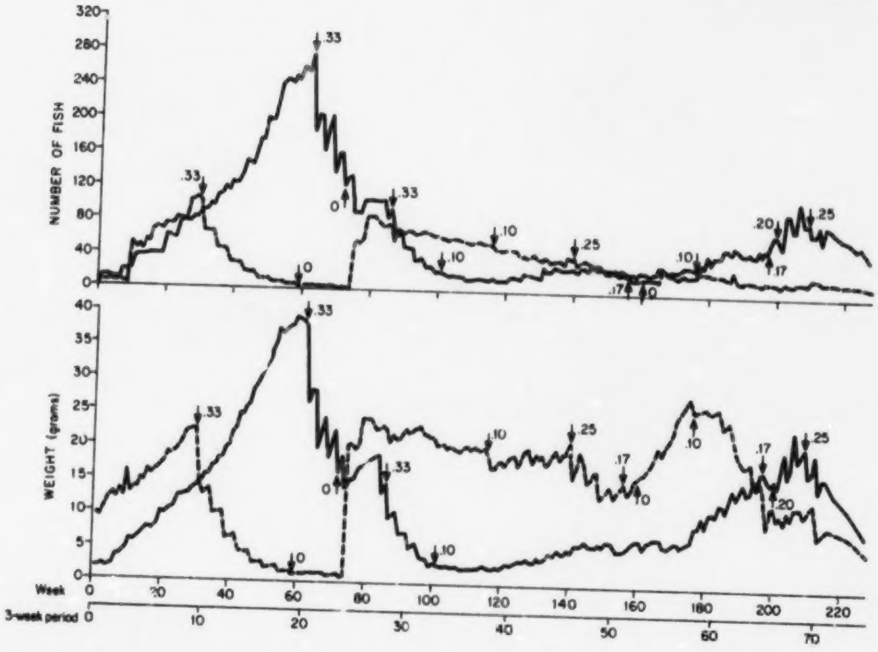

FIGURE 5.–Course of competing populations, test pair. Solid line, guppy; broken line, swordtail. Numbers indicate target exploitation rates.

(week 30), under the mistaken impression that the greater biomass then achieved by the swordtail indicated a greater productive capability. Exploitation produced a rapid decline in the swordtail to a low population level (Figure 5). Cessation of swordtail exploitation at week 59 and initiation of guppy exploitation at week 62 did not lead to recovery of the swordtail, in spite of a drastic decline in guppy abundance (Figure 5).

By week 74, it became apparent that the swordtail would require a lengthy period for recovery, even if guppy abundance were further reduced. To accelerate the study of exploitation, the populations were reconstructed during weeks 74-85, using fish from exploited populations that had been placed in a reserve tank. After reconstruction, the populations approximated fairly closely their number and weight at the time exploitation was started (compare week 85 with week 30 in Figure 5). Exploitation rates after week 85 were adjusted to keep both the guppy and swordtail at productive levels while trying as wide a range of pairs of exploitation rates as possible.

RECRUITMENT RELATIONS

Juvenile fish were counted both when removed from and returned to the adult tanks; it was thus possible to obtain a measure of recruitment. Numbers were converted to weights by use of factors (mean weights per fish) based on weighings of the juveniles: guppy, 0.0656 g based on 1,417 fish in 126 weighings spread over 199 wk; swordtail 0.0678 g, 337, 61, 196, respectively. At the beginning of the experiments, when few fish were in the nursery tanks, it was possible to distinguish individual groups of recruits by size, count them, and thereby estimate the "reproductive lag" from birth to recruitment. The lag was found to be approximately one brood interval (guppy, 3 wk; swordtail, 4 wk) for each species. In constructing the stock-recruitment relations, the recruitment for each brood interval was compared with the mean stock in the adult tanks during the preceding brood interval. During periods of exploitation, the catch was subtracted from the stock at the beginning of the interval.

Because of the great variability in the recruitment data, group means were used for both species. The basis of the grouping was an interval of 5 g (0.0-4.9, 5.0-9.9, etc.) in the adult tank stock weight. Data used in calculating recruitment curves were pairs consisting of the mean adult stock weight and mean recruit weight for each group.

The stock-recruitment data for the guppy (Figure 6) could be fitted by a Ricker (1958) curve of the type:

$$R_{N+1} = a\bar{S}_N \exp(-b\bar{S}_N),$$

where R_{N+1} is recruitment during brood interval $N+1$ and $\bar{S}_N$ is mean adult stock during brood interval N, both in grams. Fitting of the curves shown (Figure 6) was by least squares to the rectilinear logarithmic form of the relation:

$$\log_e R_{N+1}/\bar{S}_N = \log_e a - b\bar{S}_N.$$

Values of the constants are given in Table 6.

Data for the swordtail (Figure 7) did not conform well to the Ricker relation, as shown by the parabolic nature of the points for the competing stock, and were fitted better by a simple parabola:

$$R_{N+1} = a\bar{S}_N - b\bar{S}_N^2,$$

symbols as above. Curves shown (Figure 7) were fitted directly to the grouped data by least squares. Values of the constants are in Table 6.

TABLE 6.–Stock-recruitment data comparing populations of the two species with data from the relations: guppy, $R_{N+1} = a\bar{S}_N \exp(-b\bar{S}_N)$; swordtail, $R_{N+1} = a\bar{S}_N - b\bar{S}_N^2$.

Species and situation	No. of pairs of observations[1]	Constants, per brood interval		Recruitment at value of $\bar{S}_N$ for R_{max}, independent situation (g)	
		a	b	Per brood interval[2]	Per week
Guppy:					
Independent	76	0.343	0.061	2.07	0.69
Competing	117	0.092	0.028	0.95	0.32
Swordtail:					
Independent	32	0.229	0.007	1.90	0.48
Competing	86	0.066	0.003	0.42	0.10
Total	311				

[1] In fitting curves, data were grouped by 5-g intervals of $\bar{S}_N$.
[2] Guppy, 3 wk; swordtail, 4 wk.

Comparison of results for the two species **(Figures 6, 7; Table 6) reveals both similarities and** differences. Despite the different types of recruitment curves, there is the suggestion in both species that maximum recruitment occurs at intermediate rather than very high or very low adult stock levels, as has been observed for other species (Ricker 1958; Silliman 1969b). Also, recruitment for both species was depressed by competition. However, the depression was greater for the swordtail, as shown in the comparison of standardized recruitment (last column, Table 6). This is in keeping with the finding to be reported below that the guppy is more productive than the swordtail. This finding is also supported by the fact that guppy recruitment was greater than swordtail recruitment in both independent and competing situations (last column, Table 6).

Some additional information on recruitment was obtained from a study of count discrepancies. Because all additions to and removals from the adult tanks were recorded, it was possible to calculate an "expected" count (the previous count

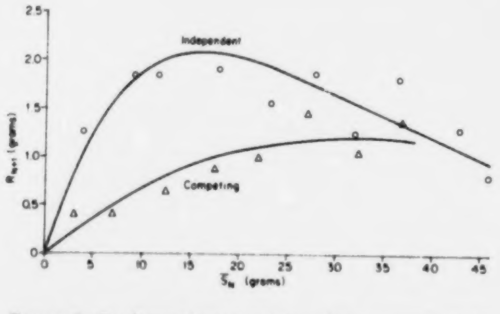

FIGURE 6.–Stock-recruitment relation for the guppy. Data grouped by 5-g intervals of $\bar{S}_N$. N is the number of the 3-wk brood interval.

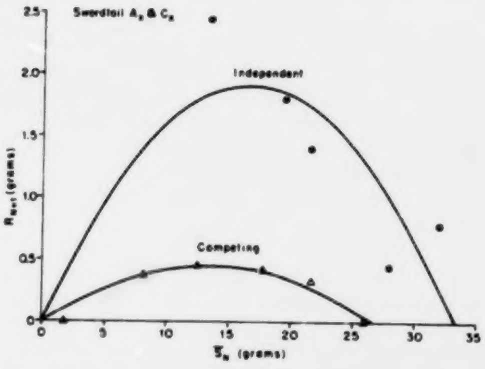

FIGURE 7.–Stock-recruitment relation for the swordtail. Data grouped by 5-g intervals of $\bar{S}_N$. N is the number of the 4-wk brood interval.

plus recruits and minus catch and deaths) to be compared with the actual counts made. Some of the observed discrepancies were no doubt due to unobserved deaths (dead fish eaten by others before seen) or to errors in counting. That some errors occurred is not surprising. Each expected-actual comparison involved as many as 17 separate counts. During each main count while exploiting the stocks the counter had to keep in mind the total number, the number caught, the state of maturity of each fish, and the sex of each mature fish.

The distribution of discrepancies for selected (to provide representative data) periods (Table 7) shows that negative discrepancies (actual less than expected) exceed the positive for both swordtails and guppies. This no doubt arose from the unrecorded natural mortalities mentioned above. The two positive discrepancies for the swordtail probably represent counting errors. For the guppy, however, the fairly large proportion of positives exceeding three fish suggests that unrecorded recruitment occurred. Apparently some of the guppy "fry" escaped detection, even though a thorough search of the tanks was made. This phenomenon is in keeping with the observed greater hardiness of the guppy, and suggests that the superiority in recruitment for the guppy was even greater than indicated in the stock-recruitment relations reported above.

TABLE 7.–Count discrepancies for selected periods: swordtail, April 1970 to June 1972; guppy, March 1970 to June 1972. Values represent "expected" number subtracted from the actual count.

Discrepancy	Swordtail	Guppy
−20	—	1
−12	—	1
−11	—	—
−10	3	1
−9	—	2
−8	2	1
−7	2	1
−6	1	1
−5	3	—
−4	3	2
−3	3	1
−2	1	3
−1	2	3
0	1	2
+1	1	3
+2	—	1
+4	—	1
+5	—	1
+6	—	3
+7	—	1
+8	—	2
+9	1	—
Total	23	31

SIMULATION MODEL

Mathematical Derivation

Data of population weight reflect growth of individual fish as well as recruitment and mortality, and all of the analyses below will be in terms of weight. Development of the formulae requires a fairly extensive list of symbols, which are defined below.

P = Total population weight in grams.
t = Time from start, in 3-wk periods.
X = Fishing effort in arbitrary units.
q = Catchability coefficient.
F = Instantaneous rate of fishing mortality ($=qX$).
m = Three-week rate of fishing mortality.
G = Constant of the Gompertz growth curve.
k = Constant of the Gompertz growth curve and of the Fox (1970) population model.
c, h, j = Empirical constants.

Adding a term for the effect of fishing to the formulae of Volterra (1928) gives a pair of differential equations:

$$dP_1/dt = f(P_1) - f(P_2) - f(X_1), \qquad (1)$$

$$dP_2/dt = f(P_2) - f(P_1) - f(X_2). \qquad (2)$$

In these equations, the first term of the right hand side is for population growth; the second, for competition; and the third, for the effect of fishing. The development is exactly parallel for the two equations, and only that for Equation (1) will be outlined below.

For the growth term Volterra (1928) used $f(P_1) = j_1P_1 - h_1P_1^2$. This is the logistic growth curve, which requires symmetrical population growth. Growth for the guppy under fishing (equilibrium yield) was shown by Silliman and Gutsell (1958) and Silliman (1968) to be distinctly asymmetrical. The Gompertz (1825) curve, introduced as a population yield model by Fox (1970), is suitable for asymmetrical growth and will be shown in the section on determination of constants to be suitable for initial population growth in both the guppy and the swordtail. This is expressed:

$$P_t = P_0 \exp\,[G - G\exp\,(-kt)]. \qquad (3)$$

It can be shown by mathematical analysis of

Equation (3) that the limit $P_\infty = P_0 \exp(G)$, and by substituting this in Equation (3), differentiating and taking logs a growth term may be derived for Equation (1):

$$f(P_1) = P_1 k_1 (\log_e P_{1\infty} - \log_e P_1). \tag{4}$$

For the competition term, Volterra (1928) used $f(P_2) = c_1 P_1 P_2$. Preliminary experimentation showed that this term was unsatisfactory for the guppy-swordtail experiments, since it was impossible to obtain even a reasonably good fit using it. I also experimented with $f(P_2) = c_1 (P_1 + P_2)$ on the theory that the sum of the populations, rather than their product, might be controlling, but it was equally unsatisfactory. The most suitable term proved to be simply:

$$f(P_2) = c_1 P_2. \tag{5}$$

This term agrees with the reasonable idea that the competitive effect on one population is proportional to the size of the other.

For the fishing term I adopted from Fox (1970):

$$f(X_1) = q_1 X_1 P_1 = F_1 P_1. \tag{6}$$

Substitution of Equations (4), (5), and (6) in Equation (1) provides the model for the first population:

$$dP_1/dt = P_1 k_1 (\log_e P_{1\infty} - \log_e P_1) - c_1 P_2 - F_1 P_1. \tag{7}$$

By exactly parallel derivation the model for the second population is:

$$dP_2/dt = P_2 k_2 (\log_e P_{2\infty} - \log_e P_2) - c_2 P_1 - F_2 P_2. \tag{8}$$

Thus the model for the competing populations represents a modification of the Fox (1970) expoential surplus-yield model, with the addition of a term for competition.

Determination of Constants

Growth data were obtained from the independent populations. Gompertz (1825) curves were fitted to the initial growth period for both species (Figures 8, 9), using the analog computer method of Silliman (1967). Asymptotic levels were 38.7 g for the guppy and 33.7 g for the swordtail. These values were used for the zero exploitation levels in fitting the Fox (1970) model. The zero points plus two other exploitation rates (relatively stable periods considered to be equilibrium points: guppy, weeks 316-334 and 355-373, Figure 2; swordtail, 322-334 and 342-354, Figure 3) gave three fitting points for each species (Figures 10,

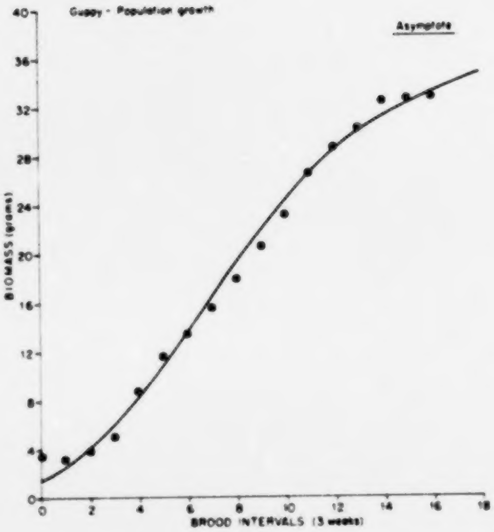

FIGURE 8.–Initial growth for the independent population of the guppy, with fitted Gompertz curve.

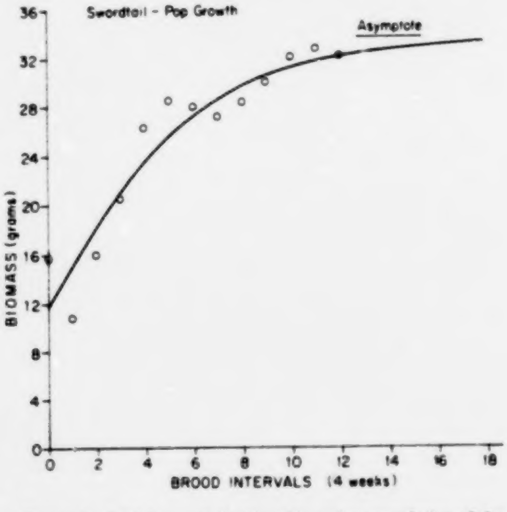

FIGURE 9.–Initial growth for the independent population of the swordtail, with fitted Gompertz curve.

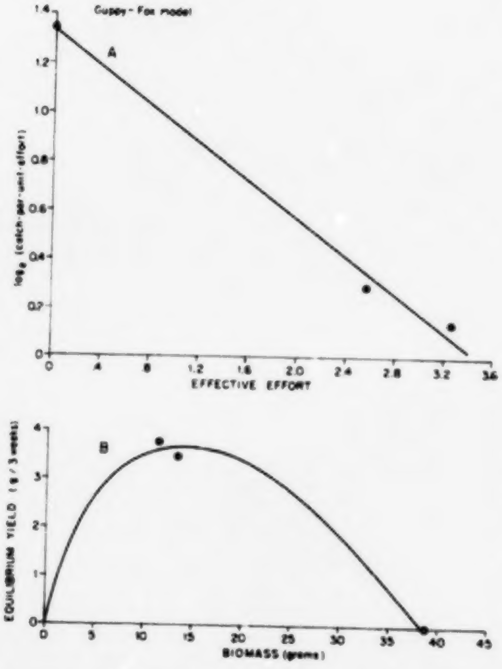

FIGURE 10.—Fox (1970) model fitted to yield data for the guppy. Exploitation rates are 0.000, 0.257, and 0.326 per 3-wk period (left-to-right in upper panel, reversed in lower panel).

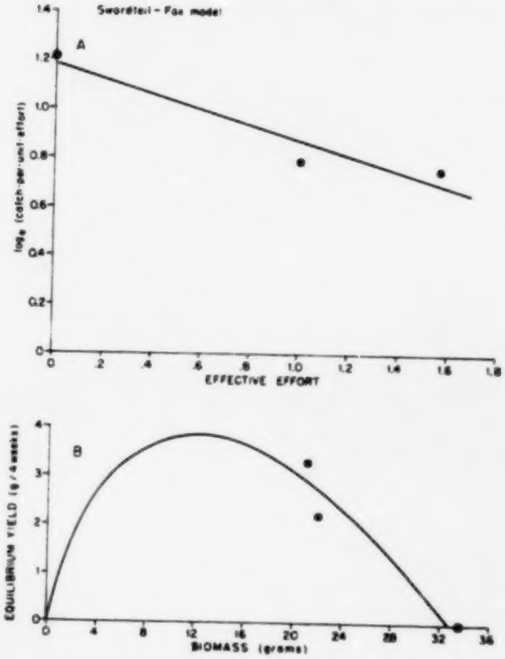

FIGURE 11.—Fox (1970) model fitted to yield data for the swordtail. Exploitation rates are 0.000, 0.100, and 0.157 per 4-wk period (left-to-right in upper panel, reversed in lower panel).

11). Effective exploitation rates shown varied slightly from the "target" rates because of lack of infinite divisibility of the populations and because of errors. The fitted Fox models yielded values of k of 0.260 per 3 wk and 0.321 per 4 wk for the guppy and swordtail, respectively. Comparable values for the Gompertz curves were 0.193 and 0.260. It was considered more appropriate to use the values from the Fox model because the analyses were based on that model. To place the swordtail on the same time scale as the guppy, the value of k was multiplied by ¾, or ¾(0.321) = 0.241.

Data of catch and biomass for the competing populations (Table 8) were used to calculate exploitation rates. Again the effective rates varied from the target rates as explained in the preceding paragraph. Also, it was again necessary to adjust the effective rates for the swordtail to the same time scale as the guppy. This was done by the formula $m = 1 - (1 - m')^{3/4}$, where m' is the unadjusted rate. Finally, for use in the differential equations, the 3-wk rates must be converted to instantaneous rates. The formula is: $F = -\log_e(1 - m)$, from Ricker (1958).

The use of instantaneous exploitation rates as employed herein assumes that P declines continuously, whereas the experimental technique was to remove all the fish at the beginning of the brood interval. It can readily be shown, however, that the reduction in population resulting from the application of m at the beginning of a period is exactly the same as the application of the equivalent F throughout the period, even if both are superimposed on a constant natural mortality.

A summary of all the constants used in applying Formulae (7) and (8) to biomass data from the competing populations is given in Table 9. Where both unadjusted and adjusted data are shown, the latter were the ones used.

Application of the Model

Using standard analog computer techniques (Ashley 1963) values of guppy and swordtail

TABLE 8.–Exploitation of competing populations. Rates are per brood interval: guppy, 3 wk; swordtail, 4 wk.

Week	Target rate	Effective rate	Biomass (g)	Catch (g)
		Guppy		
62	0.333	0.335	38.0	12.1
65			28.3	11.1
68			24.2	7.7
71			22.5	7.0
86	0.333	0.344	14.8	5.2
89			10.4	3.7
92			7.4	2.4
95			5.9	2.0
98			3.9	1.3
101	0.100	0.113	3.0	0.4
104			2.8	0.4
107			2.7	0.5
110			2.3	0.1
113			2.5	0.1
116			2.6	0.2
119			2.6	0.1
122			3.2	0.3
125			3.5	0.1
128			4.0	0.7
131			4.2	0.5
134			4.6	0.4
137			5.3	0.4
140			5.4	0.3
143			6.2	0.6
146			6.2	0.4
149			6.3	0.7
152			6.8	0.7
155			5.4	0.4
158			6.2	0.4
161			6.8	0.8
164			6.8	0.5
167			7.1	0.8
170			6.2	0.6
173			6.1	0.7
[1]175			6.7	2.0
179			10.3	1.2
182			11.0	1.0
185			12.2	1.1
188			14.5	1.5
191			15.5	3.4
194			16.2	1.8
197	0.200	0.223	17.5	6.4
200			16.3	2.5
203			20.2	3.6
206			23.1	4.7
209	0.250	0.259	21.0	5.3
212			19.9	5.1
215			16.6	4.5
218			14.1	3.6
221			12.4	3.5
224			10.6	2.8
227			8.3	1.9
		Swordtail		
30	0.333	0.346	22.3	8.0
34			13.5	3.9
38			10.2	4.0
42			6.7	2.6
46			4.3	1.5
50			2.8	0.8
54			2.2	0.8
58			1.5	0.4
116	0.100	0.112	19.0	2.6
120			18.2	2.4
124			19.1	1.3
128			20.2	2.5
132			19.2	2.3
136			20.1	1.9
140	0.250	0.254	21.2	5.9
144			18.8	4.6
148			16.9	4.5
152			15.0	3.0
156	0.100	0.112	15.2	1.7
176	0.100	0.088	26.2	1.2
180			26.6	1.2
184			26.5	1.5
188			22.0	2.2
192			18.0	4.0
[2]197			14.4	0.2
200			12.1	1.0
204			11.5	1.3
208			12.1	1.6
212			12.8	1.7
216			9.3	1.0
220			8.6	0.8
224			7.5	0.6
228			5.6	0.5

[1] Should have been 176.
[2] Should have been 196.

biomass were simultaneously generated using Formulae (7) and (8). A number of trials were made on data from the control populations (Table 10) to find the most suitable values of the competition coefficients c_1 and c_2. Values of $c_1 = 0.071$ (guppy) and $c_2 = 0.120$ (swordtail) produced curves (Figure 12) which fitted reasonably well except for the oscillatory variations to be discussed below.

TABLE 9.–Constants used in fitting simulation model to biomass data for competing populations.

Guppy k_1 = 0.280 (3-wk) $P_{1\infty}$ = 38.2 g				Swordtail k_2 = 0.321 (4-wk) k_2 = 0.241 (3-wk) $P_{2\infty}$ = 32.7 g				
3-wk period	m_1		F_1	3-wk period	m_2			Adjusted F_2
	Target	Effective			Target	Effective	Adjusted	
20-23	0.333	0.335	0.408	9-19	0.333	0.346	0.273	0.319
29-32	0.333	0.344	0.422	38-45	0.100	0.112	0.085	0.088
33-64	0.100	0.113	0.120	46-50	0.250	0.254	0.197	0.219
65-68	0.200	0.223	0.252	51 only	0.100	0.112	0.085	0.088
69-75	0.250	0.259	0.300	58-75	0.100	0.088	0.067	0.069

TABLE 10.–Biomass levels, 3-wk means, control populations.

Period	Weight (g)		Period	Weight (g)	
	Guppy	Swordtail		Guppy	Swordtail
0	1.6	8.2	38	21.0	0.3
1	2.1	13.2	39	21.4	0.3
2	2.4	10.6	40	23.4	0.3
3	4.5	10.5	41	25.0	0.3
4	6.6	14.0	42	27.8	0.3
5	8.2	17.0	43	29.0	0.0
6	10.1	18.5	44	29.1	0.0
7	11.5	20.4	45	30.2	0.0
8	12.6	21.4	46	30.8	0.0
9	14.0	21.7	47	31.4	0.0
10	15.2	22.1	48	31.6	0.0
11	16.6	22.0	49	32.7	0.0
12	18.6	19.4	50	31.4	0.0
13	19.8	17.8	51	32.5	0.0
14	21.0	17.3	52	34.1	0.0
15	20.4	23.5	53	35.2	0.0
16	19.3	20.9	54	37.0	0.0
17	19.7	20.3	55	36.4	0.0
18	20.9	19.5	56	36.5	0.0
19	21.4	16.9	57	40.7	0.0
20	23.4	15.4	58	42.6	0.0
21	25.1	14.2	59	[1]47.3	0.0
22	27.3	13.4	60	44.1	0.0
23	29.1	12.8	61	43.9	0.0
24	30.8	11.1	62	42.4	0.0
25	32.3	10.6	63	42.7	0.0
26	32.6	9.4	64	45.5	0.0
27	32.7	8.0	65	44.4	0.0
28	32.2	7.2	66	34.4	0.0
29	32.7	5.7	67	29.7	0.0
30	32.0	4.0	68	32.5	0.0
31	30.1	3.0	69	35.8	0.0
32	27.1	2.0	70	36.7	0.0
33	24.8	1.5	71	[2]34.1	0.0
34	23.1	1.0	72	[2]30.9	0.0
35	23.3	0.9	73	[2]28.0	0.0
36	22.5	1.0	74	[2]25.5	0.0
37	21.9	0.6	75	[1,2]22.8	0.0

[1]Based on two observations.
[2]Based partly on interpolation.

TABLE 11.–Biomass levels, 3-wk means, test populations.

Period	Weight (g)		Period	Weight (g)	
	Guppy	Swordtail		Guppy	Swordtail
0	2.0	9.6	38	2.6	16.7
1	2.0	[1]12.6	39	2.5	17.9
2	3.8	13.0	40	3.1	18.4
3	5.6	14.2	41	3.4	18.5
4	6.8	14.3	42	3.7	19.5
5	7.6	16.0	43	3.8	19.2
6	9.4	17.2	44	4.4	18.5
7	10.6	18.9	45	4.9	19.5
8	12.6	20.5	46	5.2	18.9
9	13.4	22.3	47	6.2	18.6
10	15.1	13.4	48	6.3	15.9
11	16.6	11.1	49	6.1	14.5
12	18.7	8.9	50	6.6	14.0
13	21.5	6.6	51	5.4	14.5
14	25.0	4.3	52	6.1	14.7
15	27.9	3.1	53	6.5	16.5
16	30.8	2.5	54	6.8	18.3
17	35.4	2.1	55	6.8	20.6
18	37.1	1.5	56	6.2	22.7
19	38.5	1.2	57	6.4	[1]26.0
20	34.3	1.1	58	7.5	26.8
21	25.6	1.2	59	9.5	26.4
22	21.6	1.2	60	10.9	26.2
23	19.7	1.1	61	12.0	24.8
24	([2])	([2])	62	13.7	22.2
25	([2])	([2])	63	14.6	18.3
26	([2])	([2])	64	15.3	16.3
27	([2])	([2])	65	16.9	13.1
28	12.7	22.0	66	15.6	11.6
29	9.2	21.4	67	18.5	10.9
30	6.7	22.4	68	20.1	11.6
31	5.2	22.9	69	19.3	11.7
32	3.5	22.0	70	17.3	11.0
33	2.9	20.9	71	[3]16.3	[3]8.8
34	2.7	20.3	72	[3]14.2	[3]9.0
35	2.6	19.9	73	[3]12.4	[3]8.3
36	2.3	20.1	74	[3]10.5	[3]7.4
37	2.5	20.1	75	[3]8.7	[3]6.1

[1]Based on two observations.
[2]Reconstruction interval.
[3]Based partly on interpolation.

These values were used in applying Equations (7) and (8) to data from the exploited test populations (Table 11). Curves for the test populations (Figure 13) followed the general trend of the biomass levels, even though oscillatory deviations were great.

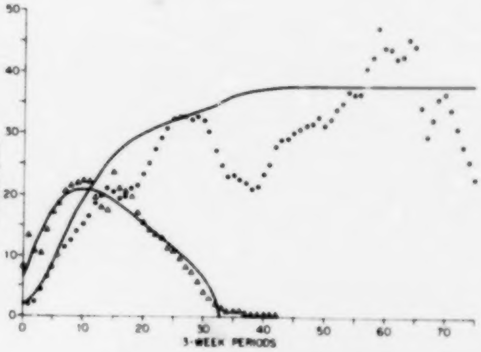

FIGURE 12.–Fitting of simulation model to control populations. Dots are for guppy, triangles for swordtail. Solid lines are fitted curves.

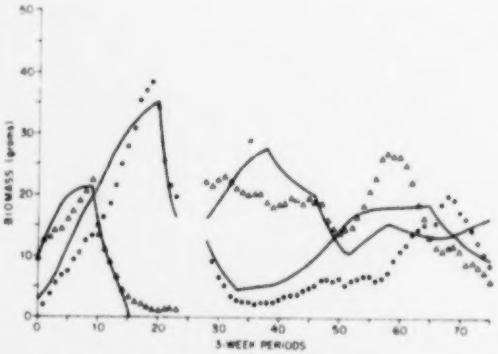

FIGURE 13.–Fitting of simulation model for test populations. Dots are for guppy, triangles for swordtail. Solid lines are fitted curves.

Oscillatory Fluctuations

The substantial oscillatory deviations evident in comparisons of observed and simulated biomass levels (Figures 12, 13) suggest the need for special study. Deviations can be evaluated more readily if they are plotted along a straight baseline (Tables 12, 13; Figure 14). Viewed in this manner, deviations appear at least roughly regular with respect to time. Also, they tend to be similar for control and test populations of the guppy for comparable periods. They did not, therefore, result solely from perturbations due to exploitation, although in the test populations deviations were somewhat greater post-exploitation than pre-exploitation.

Oscillations of the type described above seem to be basic to many populations. Walter (1973) points out that such a fluctuation occurred in Lake Michigan alewives. He developed delay-differential equations which are compatible with "an oscillatory sort of behavior centered about the equilibrium level." Although it would be of interest to apply such models to the guppy-swordtail data, it is unlikely that they would provide substantially different results insofar as the basic relations between exploitation and yield are concerned. It is with such relations that I am primarily concerned in this paper.

Since there were some fluctuations in water temperature (Figure 1) during the course of the experiments, it seemed possible that these might have caused all or part of the oscillatory population changes. To test this, a regression was erected for periods 33-75, when temperature fluctuations were fairly regular. The independent variable was water temperature, and the dependent variable was deviation of the control guppy population biomass from that predicted by the simulation model (Table 12, Figure 14). Results showed no significant correlation between biomass deviations and temperature ($r = 0.087$, $P > 0.1$).

It is worthwhile in this discussion of oscillatory

TABLE 12.–Deviations of actual biomass from theoretical, on basis of fitted model, guppy.

Period	Deviation (g) Control	Deviation (g) Test	Period	Deviation (g) Control	Deviation (g) Test
0	−0.4	−1.0	38	−15.7	−2.7
1	−0.4	−1.8	39	−15.5	−2.9
2	−1.1	−1.5	40	−13.7	−2.6
3	−0.4	−1.5	41	−12.2	−2.8
4	−0.1	−2.3	42	−9.6	−3.0
5	−0.5	−3.7	43	−8.4	−3.5
6	−0.7	−4.1	44	−8.4	−3.6
7	−1.5	−5.2	45	−7.3	−3.9
8	−2.7	−5.1	46	−6.8	−4.5
9	−3.2	−6.0	47	−6.2	−4.6
10	−3.8	−6.2	48	−6.0	−5.5
11	−4.0	−6.6	49	−5.0	−6.9
12	−3.5	−6.5	50	−6.3	−7.6
13	−3.7	−5.7	51	−5.2	−9.9
14	−3.8	−3.9	52	−3.6	−10.1
15	−5.6	−2.6	53	−2.5	−10.4
16	−7.7	−1.0	54	−0.7	−10.6
17	−8.2	2.4	55	−1.3	−10.9
18	−7.7	3.1	56	−1.2	−11.7
19	−7.9	3.8	57	3.0	−11.6
20	−6.4	−1.0	58	4.9	−10.5
21	−5.2	0.0	59	9.6	−8.6
22	−3.5	1.6	60	8.4	−7.3
23	−2.1	3.4	61	6.2	−6.3
24	−0.9	(1)	62	4.7	−4.7
25	0.3	(1)	63	5.0	−3.9
26	0.3	(1)	64	7.8	−3.2
27	0.0	(1)	65	6.7	−1.7
28	−0.8	0.2	66	−3.4	−0.9
29	−0.7	−1.2	67	−6.1	3.2
30	−1.7	−1.9	68	−5.3	5.6
31	−4.1	−1.9	69	−2.0	5.6
32	−7.4	−2.3	70	−1.1	4.6
33	−10.2	−1.8	71	−3.7	4.6
34	−12.4	−2.0	72	−6.9	3.2
35	−12.6	−2.2	73	−9.8	2.0
36	−13.7	−2.7	74	−12.3	0.8
37	−14.6	−2.7	75	−15.0	−0.7

[1] Reconstruction interval.

TABLE 13.–Deviations of actual biomass from theoretical, on basis of fitted model, swordtail.

Period	Deviation (g) Control	Deviation (g) Test	Period	Deviation (g) Control	Deviation (g) Test
0	2.2	0.1	38	0.3	−8.8
1	4.5	0.3	39	0.3	−8.0
2	−0.8	−1.8	40	0.3	−6.2
3	−3.3	−2.6	41	0.3	−5.0
4	−1.9	−4.1	42	0.3	−3.1
5	−0.6	−3.7	43	0.0	−2.6
6	−0.4	−3.3	44	0.0	−2.7
7	0.5	−2.1	45	0.0	−1.0
8	0.9	−0.8	46	0.0	−0.9
9	0.9	1.0	47	0.0	1.3
10	1.3	−2.4	48	0.0	0.7
11	1.2	−0.8	49	0.0	1.1
12	−1.2	0.1	50	0.0	2.0
13	−2.4	0.2	51	0.0	3.8
14	−2.4	0.3	52	0.0	4.0
15	4.5	2.1	53	0.0	4.7
16	2.6	2.5	54	0.0	5.6
17	2.6	2.1	55	0.0	7.1
18	2.7	1.5	56	0.0	8.5
19	0.7	1.2	57	0.0	11.2
20	0.1	1.1	58	0.0	11.4
21	−0.4	1.2	59	0.0	11.2
22	−0.4	1.2	60	0.0	11.4
23	−0.2	1.1	61	0.0	10.3
24	−1.1	(1)	62	0.0	8.0
25	−0.8	(1)	63	0.0	4.5
26	−1.2	(1)	64	0.0	2.7
27	−1.7	(1)	65	0.0	−0.2
28	−1.6	5.8	66	0.0	−1.7
29	−2.0	4.1	67	0.0	−2.4
30	−2.5	3.6	68	0.0	−1.8
31	−2.0	2.4	69	0.0	−2.0
32	−1.1	0.2	70	0.0	−3.1
33	1.5	−2.3	71	0.0	−5.7
34	1.0	−4.2	72	0.0	−6.0
35	0.9	−5.6	73	0.0	−7.1
36	1.0	−6.3	74	0.0	−3.5
37	0.8	−6.9	75	0.0	−5.2

[1] Reconstruction interval.

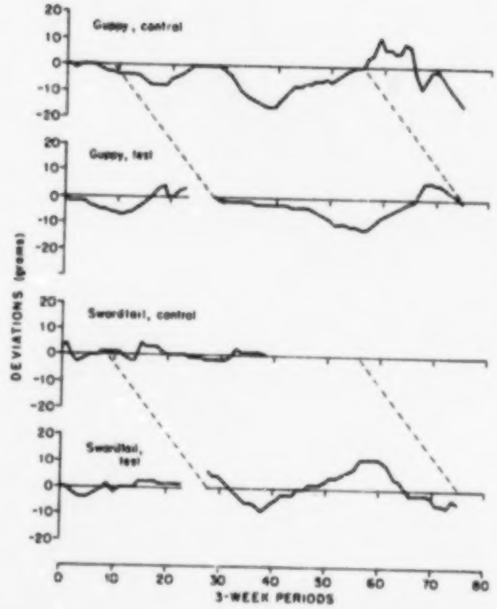

FIGURE 14.–Deviations from simulation model. Broken lines show lags for comparable portions of test and control populations.

fluctuations to consider the models fitted under independent and competing conditions. The former were based on equilibrium population conditions, whereas the latter recognized nonequilibrium conditions and used nonlinear differential equations capable of expressing continuous variation in population and yield under stable-limit cyclic variation. Conclusions for management may be different under the second type of formulation, nevertheless I feel that the conclusions drawn below are of value.

Finally, it is pertinent to discuss what seems likely to have been the start of an oscillatory fluctuation in the independent population of the swordtail. As mentioned under "Course of Populations," number and biomass increased during the final five brood intervals, contrary to what might be expected as a result of the 16.7% exploitation rate applied. The incipient oscillation may have been triggered by the low level of biomass reached just before it began, through overcompensation of the population. This level was lower than any that had been in effect since the initial growth of the population, and it may have moved the population toward the high recruitment rates shown in Figure 7.

CONCLUSIONS

Extinction of the swordtail population in the control pair (Figures 4, 12) as mentioned under "Course of Populations," is compatible with the theory of competitive exclusion first advanced by Gause (1934). He stated that where two populations are fully competing, one will have a slight advantage in growth or aggression and eventually displace the other. This occurrence illustrates one of the values of conducting population experiments over a sufficient period for natural phenomena to develop. The extinction of the swordtail could hardly have been anticipated during the first few months of the experiment, when growth of the swordtail actually outstripped that of the guppy. Gause's phenomenon of "mutual depression" (Gause and Witt 1935) also was exemplified in the experiments. Quantitative measures of this were provided by the coefficients of competition, c_1 and c_2, determined (by successive trials) for Formulae (7) and (8). These were 0.071 and 0.120 for the guppy and swordtail, respectively. These values show greater depression for the swordtail than for the guppy and, therefore, the superior competitive ability of the guppy. Growth advantage for the guppy was indicated by the values of k and P_∞ (Table 9), both of which were greater for the guppy.

My greatest interest in these experiments was to discover what combination of exploitation rates would produce the greatest sustainable yield for the two populations. This problem can be approached by calculating equilibrium yields for pairs of population sizes P_1 and P_2. At equilibrium, the left hand sizes of Equations (7) and (8) are equal to zero; with the constants already determined, F_1 and F_2 can be calculated for any pair of values P_1 and P_2. To obtain 3-wk yields, F_1 and F_2 were converted back to m_1 and m_2 by the formula $m = 1 - \exp(-F)$. Then total 3-wk yields, comparable to the yields actually obtained in the experiments (Table 8), represent the sum of m_1P_1 (guppy) and m_2P_2 (swordtail). Yields are directly comparable for the guppy, but values in Table 8 must be multiplied by three fourths for the swordtail.

I expressed the total yields ($m_1P_1 + m_2P_2$) in the form of yield isopleths (Figure 15). Inspection of

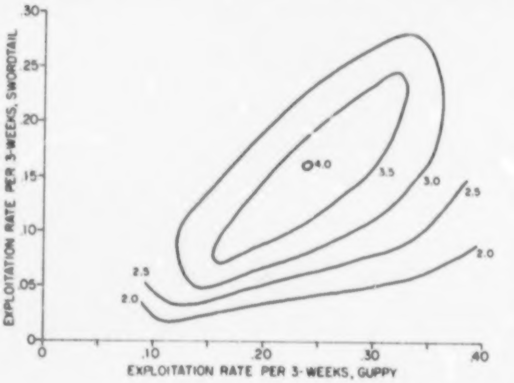

FIGURE 15.–Yield isopleths from data supplied by the simulation model. Numbers by isopleths indicate guppy yield plus swordtail yield per 3-wk period, in grams.

these isopleths reveals a ridge of high yields running roughly from $m_1 = 0.16$, $m_2 = 0.08$ to $m_1 = 0.33$, $m_2 = 0.24$. Thus, the optimal exploitation rate for the swordtail was always lower than that for the guppy, in agreement with the previously mentioned lower productive capacity of the swordtail. Also, moving from the high yield ridge toward either of the axes is moving toward lower yields. To the extent that they can be generalized, these two findings suggest that where two populations are competing, fishing both will produce greater sustainable catches than fishing either alone, provided that fishing rates are adjusted to the relative productivity of each species. The conclusion provides some support for the idea that excessive fishing of the sardine alone led to the catastrophic decline in catches in the California sardine-anchovy situation mentioned in the introduction. It is recognized that in many real fisheries, species are fished jointly by the same gear. In this case it is not possible to adjust the fishing rates separately, and results will be different (yields for a joint F will be less than for separate F's).

The maximum sustainable two-species yield, as indicated in Figure 15, is 4 g per 3-wk period, with $m_1 = 0.24$, $m_2 = 0.16$. It is of interest to see how efficiently food was used at these exploitation rates. Since juvenile fish were returned to the adult tanks from the nursery tanks, food placed in the latter must be included. During exploitation, all of the food in the adult tanks was eaten but not in the nurseries. Therefore the food consumed was between 1.0 and 1.5 times the adult amount, since food amounts for the nurseries were one-half those for the adult tanks. Three times the weekly totals of Table 1 gives 17.10 g for adult tanks only and 25.65 g for adult plus nursery tanks (weights of *Artemia* nauplii were negligible in data to two decimal places). The 4 g per 3-wk yield therefore represents food conversion efficiencies of between 0.16 and 0.23

The above efficiencies may be compared with those from the independent populations. The Fox (1970) models fitted as described under "Determination of Constants" provided estimated maximum 3-wk sustainable yields of 3.7 g for the guppy and 2.9 g for the swordtail (the latter converted from 4-wk to 3-wk basis). Food amounts were the same as for the competing populations and the comparable conversion efficiencies were 0.14 to 0.22 for the guppy and 0.11 to 0.17 for the swordtail. The range for the guppy is in reasonable agreement with the 0.20 reported by Silliman and Gutsell (1958) and 0.23 by Silliman (1968). That the guppy range is higher than the swordtail range is in keeping with other findings of superior guppy productivity reported above. Both ranges are below that for the competing populations. If significant, this difference suggests a slight gain in efficiency of the competing populations over either species growing alone.

Because the above conclusions have been derived from a mathematical model developed from the Volterra (1928) and Fox (1970) models, it is of value to refer to the work of Larkin (1963). He too used the Volterra equations as a point of departure. He applied his analyses only to hypothetical data, but his conclusions are nevertheless in general agreement with those given above. It is of interest to note his statement: "It is concluded that this formulation of interspecific competition together with variations should be applied to laboratory or natural situations to test its usefulness as a basis for prediction."

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LITERATURE CITED

ASHLEY, J. R.
1963. Introduction to analog computation. John Wiley, N.Y., 294 p.
BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 19, 532 p.
FOX, W. W., JR.
1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80-88.
FRANK, P. W.
1957. Coactions in laboratory populations of two species of *Daphnia*. Ecology 38:510-519.
GAUSE, G. F.
1932. Experimental studies on the struggle for existence. I. Mixed populations of two species of yeast. J. Exp. Biol. 9:389.
1934. The struggle for existence. Williams and Wilkins, Baltimore, 163 p.
GAUSE, G. F., AND A. A. WITT.
1935. Behavior of mixed populations and the problem of natural selection. Am. Nat. 69:596-609.
GOMPERTZ, B.
1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 115:513-585.
LARKIN, P. A.
1963. Interspecific competition and exploitation. J. Fish. Res. Board Can. 20:647-678.
LEWIS, W. M.
1963. Maintaining fishes for experimental and instructional purposes. South. Ill. Univ. Press, Carbondale, 100 p.
MACARTHUR, R. H.
1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.
MURPHY, G. I.
1973. Clupeoid fishes under exploitation with special reference to the Peruvian anchovy. Hawaii Inst. Mar. Biol., Tech. Rep. 30, 73 p.
NAGOSHI, M., R. KAWADE, S. MORI, AND D. NAKANO.
1972. On the relationship between exploitation and fluctuation in experimental fish populations. [In Jap., Engl. summ.] J. Fac. Fish. Pref. Univ. Mie 9:147-161.
PARK, T.
1962. Beetles, competition, and populations. Science (Wash., D.C.) 138:1369-1375.
RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.
SILLIMAN, R. P.
1948. Factors affecting population levels in *Lebistes reticulatus*. Copeia 1948:40-47.
1967. Analog computer models of fish populations. U.S. Fish Wildl. Serv., Fish. Bull. 66:31-46.
1968. Interaction of food level and exploitation in experimental fish populations. U.S. Fish Wildl. Serv., Fish Bull. 66:425-439.
1969a. Population models and test populations as research tools. BioScience 19:524-528.
1969b. Analog computer simulation and catch forecasting in commercially fished populations. Trans. Am. Fish. Soc. 98:560-569.
SILLIMAN, R. P., AND J. S. GUTSELL.
1958. Experimental exploitation of fish populations. U.S. Fish Wildl. Serv., Fish. Bull. 58:215-252.
VOLTERRA, V.
1928. Variations and fluctuations of the number of individuals in animal species living together. J. Cons. 3:1-51.
WALTER, G. G.
1973. Delay-differential equation models for fisheries. J. Fish. Res. Board Can. 30:939-945.

PHEROMONAL STIMULATION AND METABOLITE INHIBITION OF OVULATION IN THE ZEBRAFISH, *BRACHYDANIO RERIO*[1]

LO-CHAI CHEN AND ROBERT L. MARTINICH[2]

ABSTRACT

Female zebrafish, *Brachydanio rerio*, would not ovulate in the absence of males in waters previously inhabited by the fish. Chemical presence of males and fresh, dechlorinated tap water each induced ovulation in about half of the trials. Application of the two factors in combination gave 100% ovulation. These results suggest that in the zebrafish a pheromone released by the males stimulates ovulation and that metabolites produced by the fish repress ovulation. It is postulated that metabolites restrict spawning of the fish to the rainy season and that the pheromone functions in synchronizing reproductive readiness between sexes or in conserving courtship energy expenditure.

In a study concerning egg size, incubation period, and growth in the zebrafish, *Brachydanio rerio* (Hamilton-Buchanan), we encountered the problem of having to strip eggs from the females to synchronize the fertilization of the eggs artificially. We tried the method described by Hart and Messina (1972) without successes. We have regularly been able to induce natural spawning by introducing ripe individuals of both sexes from their holding tanks at 27°C together into a bowl of fresh, dechlorinated tap water at 21°C. Some of the changes associated with this introduction, such as the chemical presence of the males (pheromone), the physical presence of the males (visual, auditory, tactile, and lateral line), fresh tap water (absence of accumulated metabolites), and temperature shock (from 27° to 21°C), may be capable of inducing ovulation.

The roles of these factors in controlling reproduction in fishes have been well documented. Some of the examples are:

Pheromones–Aronson 1945; Tavolga 1956; Amouriq 1965; Gandolfi 1969; Rossi 1969; and Chien 1973.
Visual–Aronson 1945, 1965; Tavolga 1956; Rossi 1969; and Chien 1973.
Auditory–Tavolga 1956; Brawn 1961; Gray and Winn 1961; and Myrberg and Spires 1972.
Tactile–Egami and Nambu 1961.
Metabolites–Swingle 1956; and Greene 1966.
Temperature–Harrington 1959; Aronson 1965; and de Vlaming 1972a, b.

Much of the information in the literature, however, does not clearly distinguish between gonad development, ovulation, and spawning. The present study was undertaken to single out such ovulation-inducing factors.

MATERIALS AND METHODS

Female zebrafish were kept at 27.0 ± 1.0°C in 40- or 60-liter aerated aquaria subdivided into three or four compartments by perforated plastic dividers, one female per comparment to enable identification. Male zebrafish were isolated in aerated 20-liter aquaria at room temperature (21.0 ± 1.0°C). No visual contact was permitted between sexes. All individuals were subjected to 12 h of light per day and were generously fed "Tetramin"[3] in the morning and frozen brine shrimp in the evening. To ensure fertility, each fish was initially permitted to spawn naturally. This was done by introducing the fish into fresh, dechlorinated tap water at room temperature in a 20-cm finger bowl with another individual of the opposite sex. A total of 27 fertile females and 19 fertile males were used.

Eight experiments were designed to test the relative contribution of each factor individually, and in combination, on ovulation in the zebrafish (Table 1). In experiments 1 to 7, a female was transferred from the holding compartment into

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[1] The data in this paper were extracted from the master's thesis of R. L. Martinich.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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TABLE 1.–Design and results of experiments to test factors suspected of influencing ovulation in the zebrafish. Symbol " + " indicates presence of the factor and symbol "0" indicates absence of the factor. The chi-square values are for comparing results of any experiment with that of the control (experiment 8), and the 0.01 level critical limit is 6.63.

Item	Experiment 1	2	3	4	5	6a	6b	7	8
Factors:									
Pheromone	+	+	+	+	0	0	0	0	0
Temperature shock	0	+	+	+	+	+	+	0	0
Fresh tap water	+	+	+	0	+	+	+	+	0
Visual image of male	0	0	?	0	+	0	0	0	0
Auditory and/or lateral line stimulation	0	0	+	0	0	0	0	0	0
Number of females used	18	14	19	14	9	19	18	16	14
Results:									
Trials eggs obtained	20	15	21	8	5	17	10	7	0
Trials no eggs obtained	0	0	1	8	5	18	13	10	17
Chi-square	33.1	28.1	31.4	8.7	7.4	10.2	7.7	6.5	—
% positive responses	100	100	95	50	50	49	44	41	0

the experimental chamber for 12 to 18 h in nearly all the trials but for only 4 h in several instances in experiment 2, and then stripped by applying gentle pressure onto the abdomen. The release of ripe ova indicated that the fish had completed ovulation. Failure to give eggs, or the release of immature or ruptured eggs, was considered a negative response. Ripe ova are nearly translucent, round, and about 0.8 mm in diameter before taking on any water, and are not attached to each other. Immature ova are often opaque, may be undersized and irregularly shaped, and are often in clumps. In experiment 8, the female was stripped immediately upon removal from the holding compartment.

After successful stripping, the female was immediately permitted to spawn naturally with a male in order to assure release of all ovulated ova. After approximately 4 to 8 h, the male was removed, and the female was returned to her compartment the following day. Between experiments each female was allowed to rest for 8 to 12 days, and males 4 to 6 days.

After an unsuccessful attempt of stripping eggs, the female was presented with either male pheromone and/or fresh tap water, whatever was lacking originally in the experimental chamber, and then stripped again 4 to 18 h later. If the second stripping failed again, then the female was permitted to spawn naturally with a male. In cases where natural spawning failed, data pertaining to that female were rejected. This procedure assured that an unsuccessful attempt at stripping a female of eggs was due to the subjected treatment and not due to an unripe condition of the female.

Trials of different experiments were alternated randomly without any definite chronological sequence.

The experimental chambers in experiments 1, 2, 5, 6, and 7 were 5-liter all-glass aquaria. In experiment 3, 20-liter aquaria were used and were partitioned into two halves, one the experimental chamber and the other the male chamber. The partitionings were done with 1-mm thick opaque plastic divider perforated with holes 1.5 mm in diameter and 3 mm apart. In experiment 4, a 60-liter aquarium was used and was partitioned with nonperforated black plastic dividers into a 30-liter metabolite chamber, a 15-liter male chamber, and a 15-liter experimental chamber. Water was circulated from the metabolite chamber into the male chamber, and then to the experimental chamber and back to the metabolite chamber by means of pumping and siphoning.

The presence of the male pheromone in experiments 1 and 2 was established by air lifting into the experimental chambers water from a 5-liter aquarium into which a male was introduced simultaneously with the introduction of the female into the experimental chamber, the water then was siphoned back into the male aquarium. In experiments 3 and 4, male pheromone was provided by placing, during the experimental period, a male into the male chamber which was chemically continuous with the experimental chamber because of the perforations or water circulation.

The presence or absence of temperature shock was established by maintaining the experimental chamber respectively at room temperature (21.0± 1.0°C) or at the temperature of the holding compartments (27.0 ± 1.0°C).

The absence of metabolites in experiments 1, 2, 3, 5, 6, and 7 was attained by filling the experimental chamber and the male chamber with fresh, dechlorinated tap water. In experiment 4, metabolites were presented by conditioning the system for at least 2 wk with 75 mature zebrafish of both sexes in the metabolite chamber which is chemically continuous with the experimental chamber because of the water circulation.

Visual stimuli from a male were provided in experiment 5 by allowing the test female to be in visual contact with a mature male in a separate, chemically discontinuous all-glass aquarium. In experiment 3, the perforations of the divider partitioning the male chamber and the experimental chamber provided questionable visual stimuli from the male. In all other experiments (1, 2, 4, 6, and 7), visual stimuli from males were screened by visually isolating the experimental chambers with cardboard or black plastic sheet.

Possible auditory and lateral line stimuli from male were allowed in experiment 3 through the perforated condition of the partition separating the experimental chamber from the male chamber.

In experiment 6a, the experimental chamber was a simple 5-liter all-glass aquarium, whereas in experiment 6b a current similar to that in experiments 1, 2, 4, and 7 was provided by air lifting and back-siphoning of water between the experimental chamber and a vacated 5-liter aquarium.

Prior to each experiment, the glass aquaria and hoses were scrubbed, soaked, and thoroughly rinsed with tap water. Experiments testing the pheromonal responses utilized a different set of hoses from those used in experiments lacking the male pheromones. Different nets were used for netting males and females as a precaution against contacting a test female with the slime of a male.

RESULTS

The number of positive responses (trials eggs obtained) and negative responses (trials no eggs obtained) are given for each of the eight experiments in Table 1. The results of each experiment were compared with those of experiment 8 and the chi-square value was calculated. The percent of trials resulting in a positive response is also given for each experiment.

It is apparent from the results that presence of pheromone and absence of metabolites are the two most influential factors stimulating ovulation in the zebrafish. Experiments 1, 2, and 3 in which pheromone was provided and metabolites were absent invariably gave nearly 100% ovulation. Experiments 4, 5, 6, and 7 in which either pheromone was provided or metabolites were absent gave 40-50% ovulation. However, in experiment 8 in which pheromone was absent and metabolites were present, no ovulations were observed. The roles of metabolites and male pheromone are further indicated by the fact that females which initially responded negatively in experiments lacking the male pheromone and/or fresh tap water (experiments 4, 5, 6, and 7) gave eggs in the second stripping in all cases upon being presented with the missing factor(s).

None of the other factors tested, including temperature shock and auditory and/or lateral line stimulations seem important in controlling ovulation, as in no cases did their presence or absence significantly alter the results. The influences of water movement between the experimental chamber and the male chamber were insignificant, as there is no difference between results of experiments 6a and 6b.

Successful stripping was recorded at all times over the morning, afternoon, and early evening. After the stripping, without exception, a pair would commence natural spawning immediately upon introduction regardless of the time of day.

DISCUSSION

In the absence of the male pheromone and the presence of the metabolites, females consistently failed to ovulate (experiment 8). Under similar condition, Eaton and Farley (1974) also failed to strip eggs from isolated females. Histological studies of zebrafish ovaries by Hisaoka and Firlit (1962) indicated that oocytes are not released from the ovarian stroma into the central lumen and oviducts (ovulation) until stimulated by males during the breeding process. Eaton and Farley (1974) were able to obtain ripe ova from isolated females in the morning only after a brief (7 h) introduction of a male into the female's tank on the previous day. They suggested that the vigorous chasing behavior exhibited by the male toward the female might have provided the stimulus, although no supporting data were provided.

The results of the present study clearly establish that a male pheromone stimulates ovulation of the female. Little is known about the nature of the male pheromone. It appears not to be species specific since circulation of water between aquarium containing male *Brachydanio albolineatus* and aquarium containing female *B. rerio* elicited ovulation in the female in four out of four trials. Intrageneric interspecific effectiveness of sex pheromone has also been demonstrated by Rossi (1969) in *Colisa lalia* and *C. labiosa*. In this case a female pheromone can induce nest building in heterospecific males.

As to the chemical nature of piscine sex pheromones, Amouriq (1965) identified an estrogen as the pheromone inducing hyperactivity in male *Lebistes reticulata*, and Tavolga (1956) identified the internal fluid of the ovary as the source of the chemical stimulus eliciting courtship behavior of male in *Bathygobius soporator*. In the present study, of six trials consisting of placing test females into fresh tap water previously occupied for 24 h by a male, only four positive responses were recorded. Since the metabolites produced by a male in 24 h are far below the threshold level for inhibiting ovulation, as we have experienced and as Greene (1966) has reported, the two failures out of six trials in the above experiment suggest either that the male pheromone is short lived or that less male pheromone was released in the chemical absence of the female.

The selective advantage of an ovulating pheromone in the zebrafish is not clear. Although Hart and Messina (1972) claimed to be able to obtain sperm from male zebrafish at all times under laboratory conditions, we often encountered unsuccessful milking of males. If both sexes are not sexually ready at all times, it would be advantageous to synchronize sexual readiness between sexes. If release of the ovulating pheromone corresponds with male readiness, synchronization would be guaranteed. However, males appeared to release the pheromone quite regularly, even while in the presence of metabolites as suggested by the 50% ovulation in experiment 4. Yet, it is possible that while the metabolites may repress testicular development or spermiation and the release of the pheromone by the males, the test male introduced at the same time as the test female into the two small chambers of experiment 4 was often already sexually ready at that time and would thus release the pheromone regardless of the presence of metabolites.

Such a pheromone, if functioning in synchronization, would be advantageous for a species with a long spawning interperiod. Although female zebrafish can spawn every 1 or 2 days under laboratory conditions (Eaton and Farley 1974), the spawning interperiod in the native habitat is not known.

In some fishes, it is possible that the active chasing of the female by the male prior to spawning takes part in stimulating ovulation. An ovulating pheromone would conserve such chasing energy and therefore, be selectively advantageous.

The inhibitory effect of metabolic wastes on fish reproduction has been reported by Greene (1966) who found that an increase in metabolite concentration resulted in a decrease in the number of successful natural spawnings in the zebrafish. Lin (1935) observed that grass carp, *Ctenopharyngodon idellus*, would spawn only after a rise in the river water due to rain. Similar observations confirming the coincidence of heavy rain and spawning have been made by von Ihering and Wright (1935) and Lake (1967). Lake suggested that the stimulatory effect of rain on fish spawning was through addition of soil elements through runoffs. However, according to Swingle (1956), draining a pond crowded with goldfish or largemouth bass and refilling it subsequently with new water could induce spawning in the pond fish. One of us (Chen) had observed on numerous occasions that goldfish spawned during or after rain in outdoor concrete tanks. In these cases, spawning occurred without input of soil elements. Swingle (1956) suggested that the effect of rain was to dilute a spawning repressive factor. It is obvious from the present experiment that this repressive factor is metabolites.

Tang (1963) noted that the testes of silver carp, *Hypophthalmichthys molitrix*, would develop only after the volume of the reservoir had been increased by rain, thus suggesting that maturation of testes may be retarded by waste products from fish and that new water, or dilution of these wastes, is necessary for sexual development. It is possible that removal of the metabolites can also induce the release of the pheromone by the male zebrafish, indirectly stimulating ovulation in the females. In the present study, however, removal of the metabolites apparently had a direct effect on the females, as mere exposure of the females to fresh tap water resulted in ovulation in nearly half of the trials (experiment 7). Tang (1957) reported that female common carp inhibited from spawning by metabolic wastes would release eggs in the absence of males upon introduction of new water.

The chemical nature of the inhibiting metabolites is not known. Greene (1966) believed that they were ammonia. From the observation made by Swingle (1965) that crowding of bluegill inhibited spawning in the largemouth bass in the same pond, the inhibiting metabolites cannot be species specific.

As discussed earlier, many of the freshwater fishes in the tropics spawn only in the rainy season. During this period, there is an addition of flooded lowland suitable for the deposition of eggs, an increase in the dissolved oxygen favorable for embryological development, and an increase of organic and inorganic nutrients which promote growth of food plankton. Rain would also dilute any metabolic wastes accumulated during the dry season. In this context, metabolites may serve as a controlling factor, repressing ovulation until the rainy season when environmental conditions are more favorable for both embryo development and larval growth.

The results of the present study clearly indicate the stimulatory effect of the male pheromone and the inhibitory effect of metabolites on ovulation in the zebrafish. As gonadotropin is known to be effective in inducing ovulation in fishes, either directly, or via stimulating the synthesis of corticosteroids and/or progesterone (Donaldson 1973; de Vlaming 1974), the action of the ovulating pheromone and the metabolites is probably to activate or to deactivate the hypothalamus-pituitary-gonad axis. A pheromonal facilitation of gonadotropin-induced ovulation has been reported in mouse (Zarrow et al. 1973). Further studies are needed to clarify the route of action of the pheromone and the metabolites.

Aronson (1965) cited numerous examples in fishes in which gonadal development and subsequent spawning were stimulated by either an increase or a decrease in temperature. An increase in temperature has been reported to affect the gonadal response to treatment with gonadotropin in *Lepomis cyanellus* by Kaya (1973) and in *Gillichthys mirabilis* by de Vlaming (1972c). In the present study, a sudden decrease in temperature alone does not seem important in stimulating ovulation in the zebrafish.

In the zebrafish, visual or auditory and lateral line stimuli between sexes do not seem important in enhancing ovulation, although some of these factors may be pertinent in eliciting the proper behavior during the actual spawning act.

The onset of light alone is not sufficient to stimulate ovulation, as demonstrated by the complete failure to strip eggs during the morning hours from females tested directly from their holding compartments (experiment 8). Furthermore, these females were stimulated to ovulate later that day, after exposure to the male pheromone and fresh tap water. Ovulation and natural spawning were induced regardless of time of day. One of us (Chen) has observed natural spawning of zebrafish to commence at midnight in darkness and continue for hours. These observations conflict with all previous accounts that the onset of light is important to trigger ovulation and spawning in the zebrafish (Legault 1958; Hisaoka and Firlit 1960; Eaton and Farley 1974).

LITERATURE CITED

AMOURIQ, L.
1965. Origine de la substance dynamogene émise par *Lebistes reticulatus* femelle (Poisson Poeciliidae, Cyprinodontiforme). C. R. Acad. Sci. (Paris) 260:2334-2335.

ARONSON, L. R.
1945. Influence of the stimuli provided by the male cichlid fish, *Tilapia macrocephala*, on the spawning frequency of the female. Physiol. Zool. 18:403-415.
1965. Environmental stimuli altering the physiological condition of the individual among lower vertebrates. *In* F. A. Beach (editor), Sex and behavior, p. 290-318. Wiley and Sons, N.Y.

BRAWN, V. M.
1961. Sound production by the cod (*Gadus callarias* L.). Behaviour 18:239-255.

BREDER, C. M., AND D. E. ROSEN.
1966. Modes of reproduction in fishes. Natural History Press, Garden City, N.Y., 941 p.

CHIEN, A. K.
1973. Reproductive behavior of the angelfish *Pterophyllum scalare* (Pisces: Cichlidae). II. Influence of male stimuli upon the spawning rate of females. Anim. Behav. 21:457-463.

DE VLAMING, V. L.
1972a. Environmental control of teleost reproductive cycles: A brief review. J. Fish Biol. 4:131-140.
1972b. The effects of temperature and photoperiod on reproductive cycling in the estuarine gobiid fish, *Gillichthys mirabilis*. Fish. Bull., U.S. 70:1137-1152.
1972c. The role of the endocrine system in temperature-controlled reproductive cycling in the estuarine gobiid fish, *Gillichthys mirabilis*. Comp. Biochem. Physiol. 41A:697-713.
1974. Environmental and endocrine control of teleost reproduction. *In* C. B. Schreck (editor), Control of sex in fishes, p. 12-83. Va. Polytech. Inst. and State Univ.

DONALDSON, E. M.
1973. Reproductive endocrinology of fishes. Am. Zool. 13:909-927.

EATON, R. C., AND R. D. FARLEY.
1974. Spawning cycle and egg production of zebrafish, *Brachydanio rerio*, in the laboratory. Copeia 1974:195-204.

EGAMI, N., AND M. NAMBU.
1961. Factors initiating mating behavior and oviposition in the fish, *Oryzias latipes*. J. Fac. Sci. Univ. Tokyo, Sect. IV, Zool. 9:263-278.

Gandolfi, G.

1969. A chemical sex attractant in the guppy, *Poecilia reticulata* Peters (Pisces, Poeciliidae). Monit. Zool. Ital. 3:89-98.

Gray, G. A., and H. E. Winn.

1961. Reproductive ecology and sound production of the toadfish, *Opsanus tau*. Ecology 42:274-282.

Greene, G. N.

1966. A reproduction control factor in the cyprinid fish, *Brachydanio rerio*. FAO (Food Agric. Organ. U.N.) Fish. Rep. 44(4):86-92.

Harrington, R. W., Jr.

1959. Effects of four combinations of temperature and daylength on the ovogenetic cycle of a low-latitude fish, *Fundulus confluentus* Goode & Bean. Zoologica (N.Y.) 44:149-168.

Hart, N. H., and M. Messina.

1972. Artificial insemination of ripe eggs in the zebra fish, *Brachydanio rerio*. Copeia 1972:302-305.

Hisaoka, K. K., and C. F. Firlit.

1960. Further studies on the embryonic development of the zebrafish, *Brachydanio rerio* (Hamilton-Buchanan). J. Morphol. 107:205-225.

1962. Ovarian cycle and egg production in the zebrafish, *Brachydanio rerio*. Copeia 1962:788-792.

Kaya, C. M.

1973. Effects of temperature on responses of the gonads of green sunfish (*Lepomis cyanellus*) to treatment with carp pituitaries and testosterone propionate. J. Fish. Res. Board Can. 30:905-912.

Lake, J. S.

1967. Rearing experiments with five species of Australian freshwater fishes. I. Inducement to spawning. Aust. J. Mar. Freshwater Res. 18:137-153.

Legault, R.

1958. A technique for controlling the time of daily spawning and collecting of eggs of the zebra fish, *Brachydanio rerio* (Hamilton-Buchanan). Copeia 1958:328-330.

Lin, S. Y.

1935. Life history of waan-ue, *Ctenopharyngodon idellus* (Cuv. & Val.). Lingnan Sci. J. 14:271-274.

Myrberg, A. A., Jr., and J. Y. Spires.

1972. Sound discrimination by the bicolor damselfish, *Eupomacentrus partitus*. J. Exp. Biol. 57:727-735.

Rossi, A. C.

1969. Chemical signals and nest-building in two species of *Colisa* (Pisces, Anabantidae). Monit. Zool. Ital. 3:225-237.

Swingle, H. S.

1956. Determination of balance in farm fish ponds. Trans. North Am. Wildl. Nat. Resour. Conf. 21:298-322.

Tang, Y. A.

1957. The effect of the "repressive factor" on fish reproduction. [In Chin.] China Fish. Mon. 57:2-3.

1963. The testicular development of the silver carp, *Hypophthalmichthys molitrix* (C. & V.), in captivity in relation to the repressive effects of wastes from fishes. Jap. J. Ichthyol. 10:24-27.

Tavolga, W. N.

1956. Visual, chemical and sound stimuli as cues in the sex discriminatory behavior of the gobiid fish, *Bathygobius soporator*. Zoologica (N.Y.) 41:49-64.

von Ihering, R., and S. Wright.

1935. Fisheries investigations in northeast Brazil. Trans. Am. Fish. Soc. 65:267-271.

Zarrow, M. X., B. E. Eleftheriou, and V. H. Denenberg.

1973. Sex and strain involvement in pheromonal facilitation of gonadotrophin-induced ovulation in the mouse. J. Reprod. Fertil. 35:81-87.

ACTIVITY, MOVEMENTS, AND FEEDING BEHAVIOR OF THE CUNNER, *TAUTOGOLABRUS ADSPERSUS*, AND COMPARISON OF FOOD HABITS WITH YOUNG TAUTOG, *TAUTOGA ONITIS*, OFF LONG ISLAND, NEW YORK[1]

Bori L. Olla, Allen J. Bejda, and A. Dale Martin[2]

ABSTRACT

Field observations off Long Island, N.Y., using scuba and ultrasonic tracking, showed the cunner, *Tautogolabrus adspersus*, to be active during the day and inactively lying in shelter at night. Fish restricted their movements during the day, remaining within 2 m of the structure providing the nighttime shelter. The fish overwinter within their home territory in a torpid, nonfeeding state. Cunner fed primarily on invertebrates, foraging both benthically and in the water column. Competition between cunner and young tautog, *Tautoga onitis*, for *Mytilus edulis* was apparent during May-June when it is the major food item for both species. But beginning in July and extending through October, while tautog continued to feed primarily on mussels, cunner shifted to a diet consisting mainly of the isopod, *Idotea baltica*.

Almost any bottom relief, natural or man-made, including rock outcroppings, piers, pilings, and boat docks, provides the basic physical structure for temperate-water reef communities of fishes. While not as diverse in the number of residents as tropical and subtropical coral reefs, these communities represent an important component of the inshore marine resources of the Atlantic coast of North America. The cunner, *Tautogolabrus adspersus*, is a prominent member of temperate-water reef communities. This ubiquitous inshore species ranges from northern Newfoundland to the mouth of Chesapeake Bay (Leim and Scott 1966) and between Cape Cod and Delaware Bay is often found co-residing with the tautog, *Tautoga onitis*, the only other labrid inhabitant of the region. The close relationship of the cunner to inshore structures makes the species highly available to the angler while at the same time placing the fish in proximity to the potential effects of inshore pollution.

Our aim in this study was to describe daily and seasonal movements of the cunner as well as their feeding habits as compared with those of young tautog of similar size.

MATERIALS AND METHODS

Observations of activity and movements of the cunner were made indirectly by ultrasonic tracking of individual fish and directly with scuba. The detailed procedures used in capturing, handling, and tracking individual fish have been described by Olla et al. (1974). The ultrasonic transmitters, manufactured by Chipman Instruments,[3] (Henderson et al. 1966) measured 30 × 9 mm and emitted pulsed signals at frequencies of 58 to 70 kHz. These were attached externally to the fish by monofilament line passed through the dorsal musculature just below the midpoint of the dorsal fin. The transmitters were made neutrally buoyant by the addition of a styrofoam collar encased in silicone.

Eight fish were captured and tracked at one of three locations (Sites A, B, and C; Figure 1) in the west end of Great South Bay, Long Island, N.Y., during July and August 1973. Site A was the end of a small peninsula with 0.2- to 0.6-m diameter riprap covering the bottom from 1.2 m above the high water mark extending out 100 m. Water depth ranged from 2.0 to 10.0 m. Site B, the Fire Island Coast Guard basin, was a 110 × 52 × 47 m open pentagon, constructed of tongue-and-groove

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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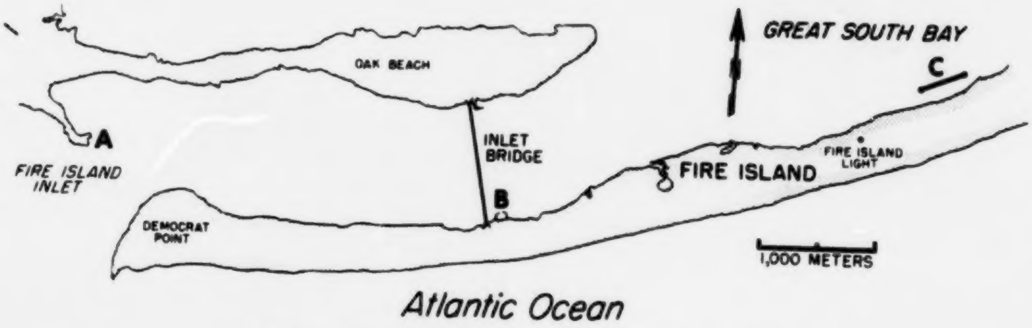

FIGURE 1.–Study area and Sites A, B, and C where cunner were tracked.

planks, steel sheeting, and piles. Water depth along the basin walls varied between 2.4 and 8.8 m with the bottom composed primarily of sand, gravel, and shell. Site C was an artificial reef, 457×46 m, consisting of submerged barges and tires on a sand and gravel bottom in 6 to 7 m of water (Briggs and Zawacki 1974).

Cunner were observed directly with scuba both day and night at weekly intervals from May through October in 1972 and 1973, and at monthly intervals from November 1972 to April 1973 for a total of 200 h (150 h daytime; 50 h nighttime).

Cunner and tautog were collected weekly, May through October at Site A for food habit analysis. The fish were either speared by scuba divers or trapped, and specimens were preserved in 10% Formalin. The contents of the entire digestive tract were examined, the food was identified, and its volume measured (Windell 1968).

RESULTS

Daily Activity and Movements

All fish tracked (Table 1) were active during the day and inactive at night. Tagged fish initiated daytime activity 16 to 41 min following the start of morning civil twilight; cessation of activity occurred 5 to 55 min before the end of evening civil twilight (Table 2). Direct scuba observations confirmed that the fish were active by day and inactive during the night. During the night, the fish were lying against, in, under, or between bottom or vertical structures. While the fish were quiescent at night, general responsiveness was low as indicated by divers being able to touch or capture fish with a hand-held net.

TABLE 1.–Release site, tracking duration, and the maximum distance traveled along the shelter site structure.

Cunner no.	TL (mm)	Release site[1]	Release date	Release time	Tracking duration (h)	Distance traveled (m)
1	190	B	7/10/73	1010	70.8	50
2	197	B	7/11/73	0920	46.7	50
3	172	B	7/16/73	1415	89.8	50
4	180	B	7/17/73	0935	34.9	5
5	215	B	7/23/73	1300	91.0	30
6	200	C	7/31/73	0937	70.8	75
7	220	C	8/ 6/73	1345	90.8	150
[2]8	220	A	7/24/73	0932	69.0	25

[1] Refers to Figure 1.
[2] Track intermittent.

TABLE 2.–The onset (minutes after morning civil twilight) and the end (minutes before evening civil twilight) of the daily activity of individual cunner as determined by ultrasonic tracking.

Cunner no.	Time	Day 1	Day 2	Day 3	Day 4	Day 5
1	Morning	—	36	34	20	—
	Evening	55	22	23	—	—
2	Morning	—	22	16	—	—
	Evening	37	39	—	—	—
3	Morning	—	22	24	34	18
	Evening	37	30	26	34	—
4	Morning	—	31	—	—	—
	Evening	44	41	—	—	—
5	Morning	—	28	—	29	25
	Evening	16	—	15	21	—
6	Morning	—	39	41	25	—
	Evening	42	35	43	—	—
7	Morning	—	26	31	27	24
	Evening	19	13	20	5	—

All of the fish tracked (Table 1) were highly localized in their daily movements, remaining within 2 m of the structures affording cover. The maximum distance traveled by any of the fish along structures ranged from 5 to 150 m.

Due to extreme ambient interference of the transmitter signal encountered during adverse water conditions, cunner no. 8 (Table 1) was tracked intermittently. When tracking was possible, the fish exhibited the same movement pattern as the other seven fish. All observed movements were restricted to the area of riprap surrounding the release point and did not exceed 25 m from the release point.

While using scuba, we were able to sight three of the tagged fish directly (no. 1, 2, and 4; Table 1). They were feeding and appeared to be normally responsive. The attached transmitter had no apparent effect on orientation or swimming ability.

Seasonal Activity

In late fall, when water temperatures dropped to 5° to 6°C, cunner were observed to be inactive and torpid, lying in cracks and crevices both day and night, similar to what Green and Farwell (1971) described for cunner in Newfoundland and what we described for young tautog (Olla et al. 1974). Some of these fish were covered with a fine layer of silt. Examination of digestive tracts from 17 torpid fish indicated that they were not feeding. The fish remained torpid throughout the winter with water temperatures ranging from 2.5° to 5.0°C until the early spring when they became active as the water temperature rose above 6°C.

Feeding

Cunner generally occur in loosely formed aggregations and feed primarily as individuals rather than in any organized social grouping. One exception to this is the social interaction and facilitation which occur when one or more fish come upon a particularly abundant concentration of food. An increase in the intensity of feeding above that which constitutes the normal grazing, picking, and searching activity serves to attract cunner from the surrounding areas. As the number of fish attracted to the feeding area increases, so does the intensity of feeding, serving to attract more and more fish until the food has been consumed. On a number of occasions (30-40), after placing a clump of *Mytilus edulis* with crushed shells at a particular place on the bottom, we have observed the attraction of 50 or more cunner within 1 to 2 min after the first few fish had found the food and begun to feed.

Cunner feed both in the water column and benthically. When feeding in the water column with a current present, the fish face into the current while maintaining position and visually scanning for suspended food items. Water column foraging is typified by high frequency of eye and head movements as the fish search in all directions. When a food item is sighted, the fish swims to it, grasps the item, and then returns to the original search posture. Fish often search the water column while remaining in close proximity to objects affording cover from the full force of the current. Only after sighting a food item does the fish move into the current to ingest it and then return to its searching position. In this manner, the fish effectively conserves energy otherwise required to maintain its position in the current between ingestions. Discontinuities of the bottom, while providing cover from the current, also act to cause turbulence and upwellings, aiding in separating and spreading the food items. Fish may feed in this manner during the day for an entire tidal cycle, the duration and frequency depending both on food density and level of satiation. A typical food item which cunner may be ingesting during this type of feeding and which occurred in significant quantities in stomach samples was the isopod, *Idotea baltica* (Table 3). This species may occur free floating, attached to bits of flotsam, such as algae or eel grass, or on fixed substrates.

In situations where there is little or no current, cunner search the water column by actively moving. There is a general dispersal and lack of any particular directional orientation in the absence of a current which is similar to Stevenson's (1972) observations of reef inhabitants at Bimini.

When feeding on bottom or vertical substrates, the fish, exhibiting a high intensity of eye movements, visually search the forage area, their snouts touching or within several centimeters of

TABLE 3.—Contents of cunner and tautog digestive tracts.

	Percent of total contents[1]					
	Cunner			Tautog		
Item	May-June	July-Aug.	Sept.-Oct.	May-June	July-Aug.	Sept.-Oct.
Mytilus edulis	57.1	4.3	13.0	74.3	87.9	83.1
Idotea baltica	0.5	72.1	61.7	4.6	2.7	—
Microcrustaceans[2]	4.4	—	—	0.5	—	—
Cirripeds	0.2	1.6	1.9	15.3	2.7	7.4
Brachyurans	13.4	2.0	10.9	4.2	3.6	5.9
Fish remains	11.8	18.1	10.6	—	—	—
Debris	7.6	1.9	1.9	1.1	3.1	3.6
Fish eggs	0.4	—	—	—	—	—
Gastropods	1.2	—	—	—	—	—
Carideans	3.2	—	—	—	—	—
No. fish	31	21	12	14	12	13
TL (mm)	63-215	106-240	154-223	105-254	136-260	177-235

[1] Determined by volume (Windell 1968).

[2] Amphipods, copepods, and mysids.

the substrate surface. On a vertical substrate, they may swim up and down and from side to side, slowly searching an encrusted pile or bulkhead wall for food. When a food item is sighted, the fish grasps and ingests it as well as some of the encrustations, ejecting much of the excess. Foraging in this manner, the fish may cover an area of no more than 4 to 5 m^2 until satiated. Similar search patterns occur along the bottom or in close proximity to rocks, logs, and other structures.

When feeding on *M. edulis*, which comprise a significant part of their diet during part of the year (Table 3), the fish grasp and ingest with the anterior canine teeth, then crush the shell with their pharyngeal teeth in much the same manner as described for tautog (Olla et al. 1974).

Food Habits

Our analysis of digestive tract contents showed that cunner forage on a variety of organisms (Table 3), mainly invertebrates, as has been reported previously (Richards 1963; Chao 1973). While Richards found amphipods to be the most important food item for cunner in Long Island Sound and Chao reported mussels (both *Mytilus edulis* and *Modiolus modiolus*) to occur most frequently in gut contents of fish collected at Nahant, Mass., our analysis for the sizes studied showed two major food items, *Mytilus edulis* and *Idotea baltica*, comprising 24.8% and 44.8%, respectively, of all food consumed. Our data showed a significant seasonal shift in the utilization of these two major forage species. During the May-June period, *M. edulis* predominated with 57.1% with only 0.5% *I. baltica* present. During July-August, the foraging pattern changed with *I. baltica* then being the major component of the diet at 72.1% and only 4.3% *M. edulis* present. This trend continued into the September-October period with 61.7% and 13.0% for *I. baltica* and *M. edulis*, respectively.

Examination of the digestive tract contents from young tautog (105-260 mm) showed that they were feeding predominantly on *M. edulis* throughout the feeding season (Table 3). Other items present occurred in varying and significantly lesser amounts. Olla et al. (1974) reported the same pattern in feeding for larger tautog.

DISCUSSION

Cunner and tautog, the only labrid inhabitants of north temperate waters of the western Atlantic, are often found co-residing on "reef" habitats south of Cape Cod. The geographical area in which these animals are found is beyond the northern limit for hermatypic corals. Hence, the "reef" habitat, as we define it, includes any natural or artificial structure or relief which provides a habitat for various species dependent, to some degree, on shelter sites (Smith and Tyler 1972), e.g., cracks and crevices, and also serves as a substrate for a variety of attached fauna and flora utilized as food items for resident fish.

Both cunner and tautog are active during the day and inactive at night. The inactive phase of nighttime is characterized by complete quiescence or sleep, a typical trait for labrid species in general (for examples see Hobson 1965, 1968, 1972; Starck and Davis 1966; Tauber and Weitzman 1969; Collette and Talbot 1972).

As was discussed in an earlier paper (Olla et al. 1974), the low level of responsiveness which is characteristic of the sleep phase of labrids and species of similar habit indicates that there is a reduction in the potential to avoid or escape environmental stress that may be imposed during the night.

Both of these species require shelter sites as resting places during the night sleep phase. Cunner of all sizes and tautog of less than 250 mm also appear to require a close association with objects affording shelter by day and during the winter, when they remain in a torpid condition. It is, therefore, obvious that the "reef" habitat, as a provider of shelter sites, would be a limiting factor in the population size of these two species. Any interspecific competition for shelter sites encountered by the cunner would probably be limited to tautog less than 250 mm, with both species requiring shelters of similar type and size. The amount of available shelter for coral reef species is an obvious limiting factor of population size (Sale 1972; Smith and Tyler 1972, 1973).

An attempt to attract or to increase populations of shelter-dependent species has been the development of man-made reefs using a variety of substances including automobile tires and bodies, construction rubble, sunken barges or ships, etc. (see Rickards 1973; Steimle and Stone 1973). The construction of man-made reefs would be most successful in areas in which sufficient food resources are available for the fish to be attracted or where the potentiality for food accretion would be increased by the addition of an appropriate substrate. These structures would be most effective when placed where both forage species and fish species may be recruited naturally, the only element having prevented their presence previously being the absence of the structure.

The most obvious difference in the feeding habits of cunner and tautog is the greater diversity of organisms eaten by cunner (Table 3). While *Mytilus edulis* makes up the bulk of the diet during the feeding year of the tautog, it comprises a significant part of the cunner diet only during May and June. For the remainder of the feeding year, *Idotea baltica* predominates, with a variety of other invertebrates and fish being ingested by the cunner. The food habits of these fish not only show a change of season, as in this study, but also vary widely with geographic location. Comparing the results of this study with those of Richards (1963) in Long Island Sound and Chao (1973) at Nahant, the diversity in the cunner's feeding is even more apparent.

The more diverse diet of the cunner as compared with the rather restricted one of the tautog in this particular habitat may in part be related to morphological differences between the two species. The cunner, with its narrower, more streamlined body, pointed snout, and thinner lips, is well suited for feeding on the small motile crustaceans, e.g., *I. baltica*, occurring both benthically and in the water column. Davis and Birdsong (1973) in their review of water column foraging in coral reef fishes show morphological differences distinguish water-column foragers from benthic foragers within the same family.

The depletion of specific foods such as *M. edulis* (Olla et al. 1974) in this community, would appear to be far more detrimental to tautog than to cunner. Competition for the same food items would likely occur only during May and June.

Shifts in feeding habits may relate to other variables besides obvious differences in the abundance of the forage species. For example, *I. baltica*, occurring in waters of Denmark, shift their daily rhythm of activity on a seasonal basis while held in the laboratory (Hørlyck 1973). In the spring this species is primarily nocturnal; during late spring and early summer the species becomes more active by day. The cunner, which feeds by day, ingested significantly larger amounts of *I. baltica* during approximately the same time that this species had changed to a diurnal activity pattern. Of course this is, at best, conjecture, since it is not well understood how closely these laboratory observations relate to the field and whether this species would show the same seasonal shift in such widely separated geographic locations.

All of the cunner tracked and observed directly remained within several meters of some structure. This behavior agreed with earlier observations on young tautog (≤250 mm; Olla et al. 1974). Furthermore, we found that tautog of this size and cunner of all sizes studied (50-240 mm) remained inshore during the winter in a torpid state, agreeing with the observations of Green and Farwell (1971). Apparently, the home range for cunner of this size is restricted throughout all seasons to the length and breadth of the structure to which they were originally recruited.

Offshore reefs (primarily shipwrecks) appear to support a population of older and larger cunner than are found in inshore waters. During trawl vessel surveys conducted by the Northeast Fisheries Center (see Grosslein 1969 for a description of the survey program) cunner, 21 to 42 cm, have been collected at stations approximately 100 km southeast of Cape Cod, Mass. These larger fish do not represent any significant part of the cunner population as far as is known at this time, but it is of interest that they do exist. Whether they were originally recruited to these offshore areas and remained there, or were part of an inshore population that moved offshore when reaching a certain size (as is the habit of older tautog) and then remained there, can only be surmised.

LITERATURE CITED

Briggs, P. T., and C. S. Zawacki.
1974. American lobsters at artificial reefs in New York. N.Y. Fish Game J. 21:73-77.

Chao, L. N.
1973. Digestive system and feeding habits of the cunner, *Tautogolabrus adspersus*, a stomachless fish. Fish. Bull., U.S. 71:565-586.

Collette, B. B., and F. H. Talbot.
1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 14:98-124.

Davis, W. P., and R. S. Birdsong.
1973. Coral reef fishes which forage in the water column: a review of their morphology, behavior, ecology and evolutionary implications. Helgolander wiss. Meeresunters. 24:292-306.

Green, J. M., and M. Farwell.
1971. Winter habits of the cunner, *Tautogolabrus adspersus* (Walbaum 1792), in Newfoundland. Can. J. Zool. 49:1497-1499.

Grosslein, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

Henderson, H. F., A. D. Hasler, and G. C. Chipman.
1966. An ultrasonic transmitter for use in studies of movements of fishes. Trans. Am. Fish. Soc. 95:350-356.

Hobson, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.

Hørlyck, V.
1973. Seasonal and diel variations in the rhythmicity of *Idotea baltica* (Pallas) and *Idotea granulosa* Rathke. Ophelia 12:117-127.

Leim, A. H., and W. B. Scott.
1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

Olla, B. L., A. J. Bejda, and A. D. Martin.
1974. Daily activity, movements, feeding, and seasonal occurrence in the tautog, *Tautoga onitis*. Fish. Bull., U.S. 72:27-35.

Richards, S. W.
1963. The demersal fish population of Long Island Sound. Bull. Bingham Oceanogr. Collect. Yale Univ. 18(2), 101 p.

Rickards, W. L.
1973. A bibliography of artificial reefs and other man-made fish attractants. Univ. N.C. Sea Grant Publ. UNC-SG-73-04, 21 p.

Sale, P. F.
1972. Influence of corals in the dispersion of the pomacentrid fish, *Dascyllus aruanus*. Ecology 53:741-744.

Smith, C. L., and J. C. Tyler.
1972. Space resource sharing in a coral reef fish community. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 14:125-170.
1973. Direct observation of resource sharing in coral reef fish. Helgoländer wiss. Meeresunters. 24:264-275.

Starck, W. A., II, and W. P. Davis.
1966. Night habits of fishes of Alligator Reef, Florida. Ichthyol. Aquarium J. 38:313-356.

Steimle, F., and R. B. Stone.
1973. Bibliography on artificial reefs. Coastal Plains Cent. Mar. Dev. Serv. Publ. 73-2, 129 p.

Stevenson, R. A., Jr.
1972. Regulation of feeding behavior of the bicolor damselfish (*Eupomacentrus partitus* Poey) by environmental factors. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals: current perspectives in research. Vol. 2. Vertebrates, p. 278-302. Plenum Press, N.Y.

Tauber, E. S., and E. D. Weitzman.
1969. Eye movements during behavioral inactivity in certain Bermuda reef fish. Commun. Behav. Biol. Part A 3:131-135.

Windell, J. T.
1968. Food analysis and rate of digestion. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 197-203. Blackwell Sci. Publ. Oxford, Engl.

CORRELATION OF UPWELLING INDEX AND DUNGENESS CRAB CATCH

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ABSTRACT

The statistical relationship between upwelling intensity and the annual *Cancer magister* catch is examined using techniques of time series analysis. The statistical relationships between upwelling in different years and crab catch in different years are examined. The statistic used is the correlation coefficient for varying time lag. The results correlating upwelling and crab catch indicate that time lag is short enough to demonstrate that adults are affected, and that the time lag is shorter in California than in Oregon or Washington. The crab catches appear to be cyclic with a period of 9 yr in California and 12 yr in Washington and Oregon. Possible causal mechanisms for the statistical relationships are presented. Results suggest that variations in crab catches may be due primarily to biological rather than abiotic influences.

Large fluctuations in yearly catch in the Pacific Coast Dungeness crab fishery have been observed over the years for which records were kept. The catch in some years is as low as 20% of the catch in good years. Furthermore, the fluctuations seem to be of a cyclic nature: 3 or 4 yr of low catch are often followed by 3 or 4 yr of high catch after which the same pattern occurs. Based on the fact that the variation in catch was similar along the entire west coast, the Pacific Marine Fisheries Commission (1965:38) concluded that a large-scale abiotic influence was responsible.

Many other explanations of the fluctuation in crab catch have rested on Cleaver's (1949) contention that abundance of adult crabs fluctuates widely in accordance with conditions affecting the early stages, e.g., the Pacific Marine Fisheries Commission (1965:38) suggested that seasonal currents possibly sweep the larvae to unfavorable settling areas. However, although the larvae may be more sensitive than juveniles to environmental changes and the percentage of them surviving is certainly less, there has been no experimental proof that fluctuation in abundance depends primarily on larval survival.

Peterson (1973) was the first to examine the statistical relationship between the Dungeness crab fishery and upwelling. (His paper serves as a good introduction to our work; much valuable information is not repeated here.) He compared the upwelling index developed by Bakun (1973) to the crab catch records for the years 1949 to 1972. The comparison was made for three different locations: Washington (lat. 48°N, long. 125°W), Oregon (lat. 45°N, long. 125°W), and northern California (lat. 42°N, long. 125°W).

Peterson used graphical comparison and two statistical techniques—the corner test and the contingency table—to evaluate the relationship between upwelling index (summed over the summer months) and the annual crab catch for several different lag times at each location. The conclusion was that good crab catch followed a good upwelling summer by 1½ yr in California and Oregon and ½ yr in Washington. Two aspects of these results are unexpected: 1) the short lag times and 2) shorter lag time in Washington than in California and Oregon. The short lag times seem to preclude the effect of upwelling on larval or early stages being the dominant cause of the large catch. The shorter lag time in Washington is unexpected because of the shorter generation times of most species in the marine food chain at the higher temperatures of more southerly waters.

Peterson explained the lag differences by proposing that the final molt from sublegal to legal size was the determining factor. Dungeness crabs molt later in more northerly waters (late fall in Washington, late summer in Oregon, and early summer in California). It was hypothesized that the Washington animals were molting after the summer upwelling and benefited from the increased food supply, whereas animals in more southerly waters molted prior to the increased food supply and did not benefit until the following summer molt.

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In this paper we have used a different statistical technique than Peterson's and have reached a different result regarding lag differences. We have computed the correlation coefficient for varying lag times. This technique uses higher resolution in the data than the techniques used by Peterson and results in a graphical presentation of the magnitude of correlation at each lag. The results show that significant correlation extends for longer lag times than ½ or 1½ yr and reverse the order of the difference in lag times along the coast. Also, we have used the same technique to describe the relationship between catches in different years. These results show that the primary cause of the cyclic nature of the variations may not be upwelling.

MATERIALS AND METHODS

The data used were the same as those used by Peterson (1973). The catch data are based primarily on the annual reports of the Pacific Marine Fisheries Commission and the California Department of Fish and Game (see Peterson 1973 for detailed discussion of sources). The total catch for each year (Figure 1) is believed to represent almost all that year's legal-size male crabs (Pacific Marine Fisheries Commission 1965:38). The completeness of this yearly sample makes the Dungeness crab an attractive species for analysis of population dynamics.

The upwelling index developed by Bakun (1973) is based upon measurements of atmospheric pressure. Upwelling and downwelling are the result of Ekman transport which is, in turn, due to surface winds. Bakun developed a method of estimating the intensity and direction of Ekman transport by relating the wind speed and direction to atmospheric pressure measurements. Using this method, he computed monthly averages of the component of Ekman transport perpendicular to and away from the shoreline. This upwelling index is assumed to indicate the average monthly upwelling. Peterson (1973) summed the monthly Bakun upwelling index over the summer upwelling season to compute a seasonal upwelling index (Figure 2). The upwelling indices were summed over the time periods from May through September for California.

These data were analyzed using a technique commonly employed in analysis of random processes to determine the degree to which two processes (or separated points of one process) covary. The formula used was:

$$R_{xy}(i) = \frac{1}{(n-i)} \sum_{j=1}^{n-i} x(j)\, y(j+i)/S_x S_y$$

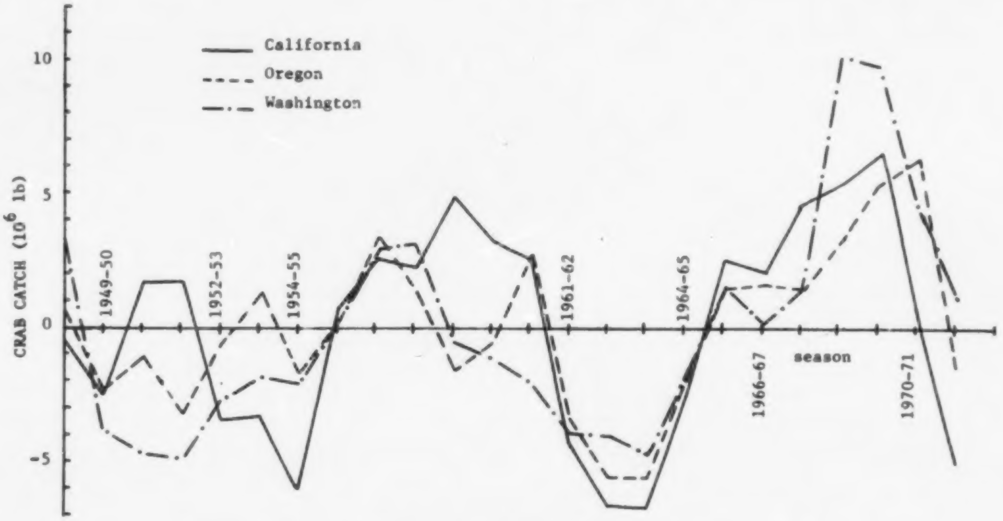

FIGURE 1.–Crab catch data for Washington, Oregon, and California (mean removed).

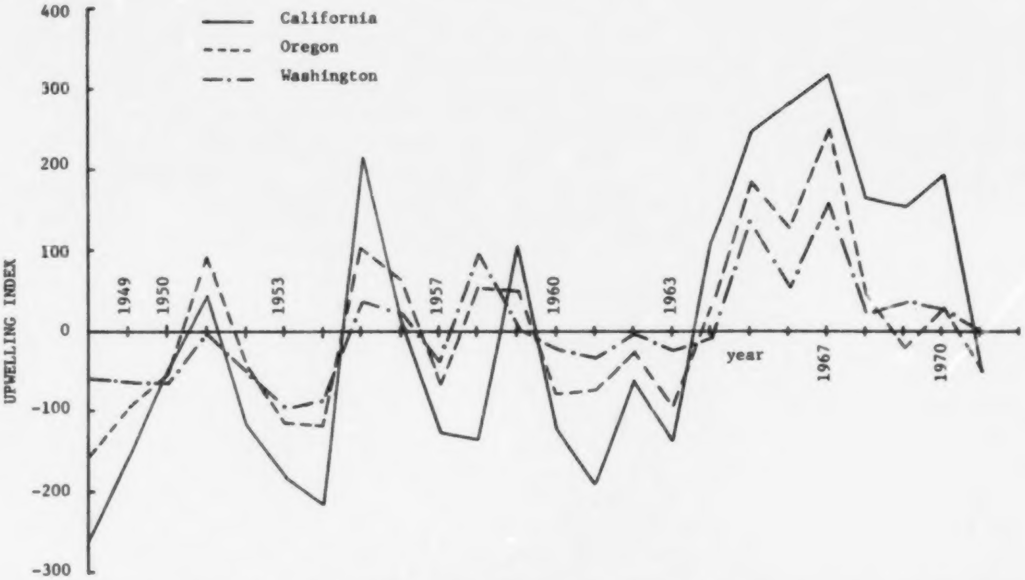

FIGURE 2.–Bakun's upwelling index for Washington, Oregon, and California (mean removed). Units are cubic meters of water upwelled per second per 100 m of coastline.

where $x(j)$ = the value of process x at time j (mean removed)

$y(j)$ = the value of process y at time j (mean removed)

S_x = the sample standard deviation of process x

S_y = the sample standard deviation of process y

n = the total number of samples.

The result of this formula is the product-moment correlation coefficient for each value of lag i. A graph of $R_{xy}(i)$ along the ordinate and i along the abscissa is termed the correlogram (Kendall and Stuart 1968). Assuming that the processes are stationary and ergodic, R_{xy} is an estimate of the expected value of the product of the two variables at each lag time. If x and y are different processes, it is termed the cross-correlation coefficient. If x and y are the same process, it is termed the auto-correlation coefficient.

Because R_{xy} is a sample statistic, the significance of its value must be considered. Although the technique is commonly used in time series analyses, the sampling theory of serial correlations has been developed only for restricted types of data (e.g., normally distributed data). Because the significance decreases as n increases, the serial correlation coefficient is usually only calculated for lags up to 30% of the total length of the data. The interpretation of our results depends only on lags of this length. However, the results are presented for lags beyond this length because they are of interest.

Another consideration in the computation of serial correlations is that of trend removal (Kendall and Stuart 1968; Ontes and Enochson 1972). Trends in the data (linear or higher order) which are not pertinent to the analysis are subtracted from the data before the correlation coefficients are computed. The trend is usually a deterministic artifact of known origin which is not present in the actual data of interest. Although upwelling, and to some extent catch data, seemed to increase over the 24 yr considered, this effect was not irrelevant to the purpose of the analysis. The results presented, therefore, include no trend removal. However, computation of the correlation coefficients was performed after trend removal and the results were similar.

RESULTS

The cross-correlation coefficients for upwelling and crab catch are plotted in Figure 3 as a function of lag time. The general shape of the function is similar for the three different locations. The coefficient for California at 0.5 yr lag is greater than for the other two. The value of the correlation coefficient for California decreases while the value increases for 1 yr at the other locations. This may indicate that high correlation exists at a shorter time lag in California than in ther other locations.

The auto-correlation coefficients for upwelling are plotted in Figure 4. Significant correlation

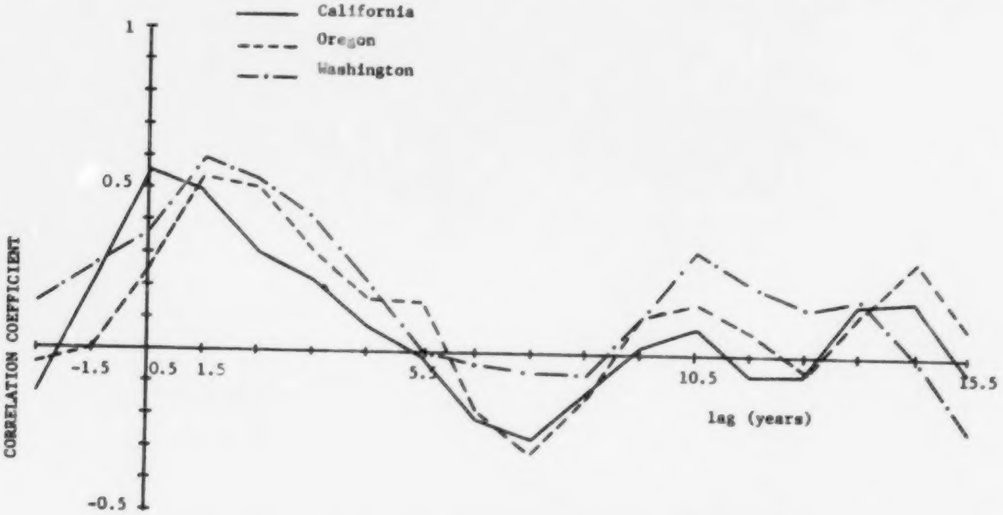

FIGURE 3.—Cross-correlation of upwelling and crab catch for Washington, Oregon, and California.

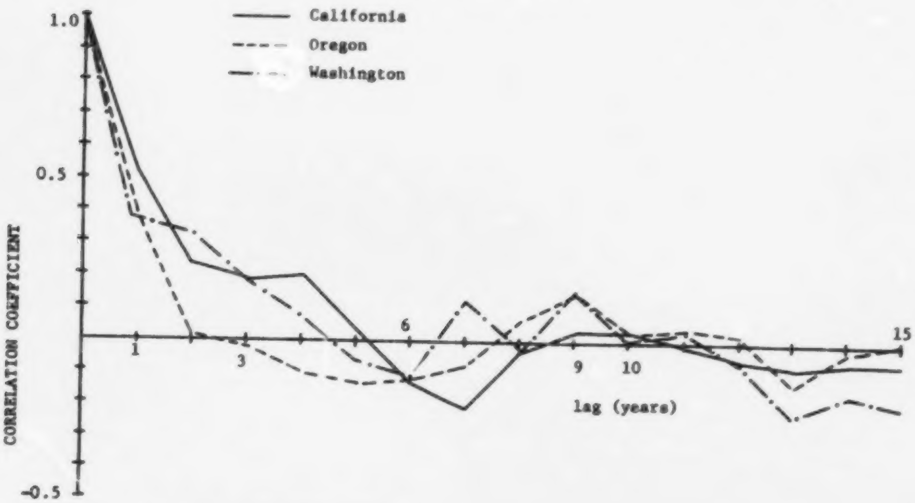

FIGURE 4.—Auto-correlation of upwelling for Washington, Oregon, and California.

exists for all three locations at a lag of 1 yr. For greater time lags no significant characteristics appear.

The auto-correlation of crab catch is plotted in Figure 5. The correlation function for each location decreases to a point of significant negative correlation. This is a characteristic of a cyclic process with a period of twice the lag value at that point. For California the period of the cycle would be 9 yr, and for Washington and Oregon it would be 12 to 13 yr. A subsequent increase to a positive correlation at a lag of twice that of the negative peak is further indication of a cyclic process. However a lag of that length is greater than 30% of the total length of the data.

DISCUSSION

These results must be interpreted in light of the general implications and limitations of statistical correlation. The correlation coefficient is used to measure the intensity of association between two variables and determine whether or not it is greater than that expected by chance alone. A high correlation coefficient serves only as an indication that a causal relationship may exist. The nature of the causal mechanism may take several forms. A high value of the correlation coefficient between two variables may be caused by one variable directly influencing the other. It may also be caused by a third variable influencing them both. Other possible alternative forms are more complicated combinations of these two. The causal mechanism may be very complex and indirect. Conclusions from the results obtained must, therefore, serve only as indications of areas of possibly fruitful investigation.

The results in Figure 3 indicate a possible relationship between upwelling and catch. The positive correlation at 0.5 yr lag which continues for several years could result from increased crab growth or survival due to increased food which may be due to nutrients provided by upwelling. The correlation at low lag time indicates agreement with Peterson's (1973) contention that adults are affected. The maximum correlation, however, appears at a shorter lag time in California than in Washington or Oregon. The fact that a significant correlation continues for an additional year may also be due to the same cause with the longer lag being the sum of the time required for the effect of nutrients to be felt at a point in the food chain in which the crab feeds plus the time required for that crab to reach a catchable size.

The cause of the apparent periodic nature of catch data indicated by Figure 5 is of primary

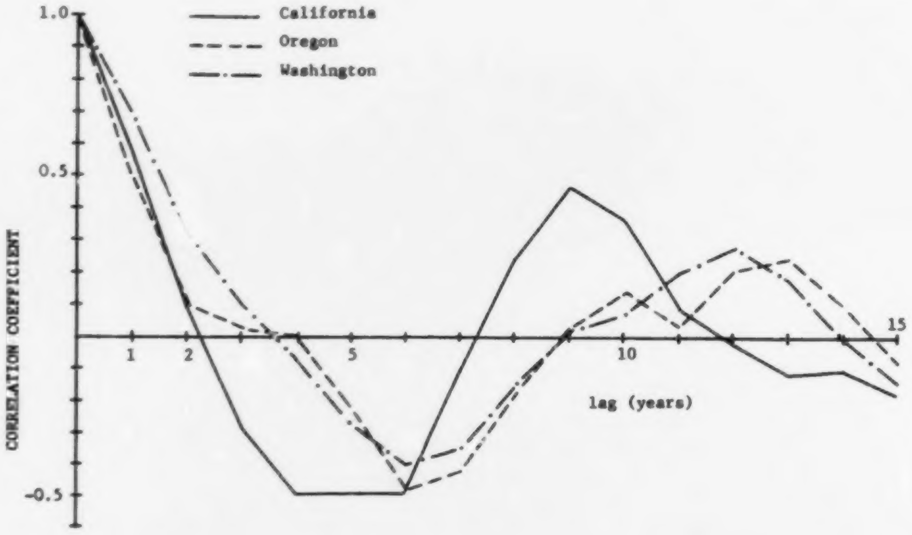

FIGURE 5.–Auto-correlation of crab catch for Washington, Oregon, and California.

concern to fisheries biologists. A possible explanation is that crab catch is merely following the cyclic upwelling. However, the auto-correlation of upwelling (Figure 4) does not indicate significant periodicity and the weak cycles suggested have different periods from those for the catches. This result may be due to the fact that the data used by Bakun (1973) were taken from four different sources covering the time periods January 1946-March 1955, April 1955-December 1959, January 1960-June 1962, and July 1962-December 1971. The data within each time period may differ by a multiplicative factor from the others but are consistent within the time period. This would affect the auto-correlation function more for longer than for shorter lags. The total effect of possible inconsistencies in the data upon the auto-correlation function is difficult to assess since the magnitudes of the multiplicative factors are not known.

A second possible explanation is that years of good catch indicate that a higher than normal percentage of the population is being caught thus depleting the adult reproductive stock. This explanation, however, is not commensurate with the widely held belief that almost all legal males are caught every year.

A third possible cause of the cyclic variations in abundance is predation. The observed cycles may be the result of interaction of crabs with a predator species. However, there is no a priori reason to expect that the period of the cycles would be slightly greater than twice the generation time. Also, the large number of predator species suggests that predation would maintain a fairly constant level unless all predator species were cycling in abundance.

A fourth possible explanation involves interactions between members of the population rather than external causes as dominant factors. Density-dependent factors which limit reproduction or growth and survival of the younger members of a population as the numbers of adults increase may cause cycles in abundance of adults. Ricker (1954) provides a discussion of density-dependent recruitment in fisheries and a simulation of time variation of abundance based on several different density-dependent recruitment relationships. One of the forms of compensatory mortality which could cause density dependent recruitment is cannibalism (Ricker 1954). Butler (1954) reported finding small Dungeness crabs (about 1 cm) among the stomach contents of older Dungeness crabs. For certain stock-reproduction curves the simulated populations oscillated in numbers. The requirements for permanent oscillation were a rapid decrease in reproduction (or survival of the young) beyond the peak of the stock-recruitment curve and mixing of generations in the breeding populations. The period of the oscillations was twice the mean length of time from parental to filial eggs.

Our results show a period of approximately 9 yr in California and 12 yr in Washington and Oregon. This would indicate a generation time of 4.5 yr in California and 6 yr in Washington and Oregon. Poole and Gotshall (1965) stated that mating occurs in California after 2.5 yr and males enter the fishery at 3.5 or 4.5 yr. Cleaver (1949) reported that in Washington maturity occurs at 3 yr and legal size occurs at the end of the fourth year. McKay and Weymouth (1935) reported that female crabs in southern British Columbia probably reach sexual maturity during the fourth or fifth year. The longer generation times in the northerly waters are commensurate with our results, although the period of the cycles indicated by our results is greater than would be expected based on Ricker's simulation and estimates of age at maturity. This disparity may be due to inaccuracies in the estimates or in our results. One possibility is an inaccurate estimate of when, in the life cycle, a major portion of reproduction occurs. If upwelling increases growth rate, the determination may have been made in good years, thereby yielding shorter time periods. A second possible explanation is inaccurate determination of the period of the cycle in our analysis. The length of the data (two or three cycles) is not adequate for accurate determination of the period of the cycle, especially when external influences appear to have caused large variations. Examination of the raw data reveals a reasonable explanation and also demonstrates correlations implied in this paper. In Figure 1, catch for northern California goes from a peak at 1950-51 or 1951-52 through a low point to a peak in 1958-59, a 7- or 8-yr cycle. It then passes through a low point and 7 yr later is again at a high point. However, instead of beginning to decrease, it rises even higher for the next several years before dropping. Figure 2 indicates that this is also the time when upwelling index is at a very high value. That the crab population reached a high density in 1965, but did not suffer the expected decline because the upwelling had provided enough food resources to sustain a larger population is a plausible explanation.

SUMMARY AND CONCLUSIONS

The correlation analysis at different lag times indicates a significant correlation of crab catch with upwelling for several years following upwelling. Auto-correlation of crab catch indicates that catch is of a cyclic nature. The same analysis of upwelling does not show a significant cyclic nature (although this may possibly be due to inconsistencies in Bakun's data). These analyses are not rigorous proofs of the indicated characteristics but rather provide impetus and direction for further research. They suggest that the cyclic variation of crab catch may be primarily due to density-dependent biotic factors rather than upwelling, although upwelling does influence catch. Further conclusions regarding the biological basis for the cyclic nature of catch data require research in the natural history and ecology of the Dungeness crab. A specific question to be answered is over what age groups are the niches similar enough for significant competition to occur. Further conclusions regarding the relationship between upwelling and catch require additional research in the nature of energy transfer from the pelagic to the benthic environment. Research in these directions may provide basis for a more dynamic fishery management policy. For instance, the importance of deciding whether the variations in crab catch are due primarily to density-dependent factors is illustrated by the implication that if competition is occurring between adults and juveniles, limited fishing of females (removing them as competitors) during years of great abundance may provide greater catches in the following years.

The statistical relationships presented also provide a basis for predicting crab catch. The values of upwelling index and crab catch over several years may be used to predict catch for the ensuing years (Rauch et al. 1975). Additional variables may be added to the basis for prediction such as temperature and results of plankton tows. This type of prediction is based on statistical relationships and does not necessarily require causal explanations of the various effects.

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LITERATURE CITED

Bakun, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

Butler, T. H.
1954. Food of the commmercial crab in the Queen Charlotte Islands region. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. 99:3-5.

Cleaver, F. C.
1949. Preliminary results of the coastal crab (Cancer magister) investigation. Wash. Dep. Fish., Biol. Rep. 49A:47-82.

Kendall, M. G., and A. Stuart.
1968. The advanced theory of statistics. Vol. 3. Design and analysis, and time-series. 2nd ed. Hafner Publishing Company, N.Y., 557 p.

McKay, D. C. G., and F. W. Weymouth.
1935. The growth of the Pacific edible crab, *Cancer magister* Dana. J. Biol. Board Can. 1:191-212.

Otnes, R. K., and L. Enochson.
1972. Digital time series analysis. John Wiley & Sons, Inc., N.Y., 467 p.

Pacific Marine Fisheries Commission.
1965. Discussion following the report on Dungeness crabs. 16th and 17th Annu. Rep. Pac. Mar. Fish. Comm., p. 38-39.

Peterson, W. T.
1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull., U.S. 71:902-910.

Poole, R., and D. Gotshall.
1965. Regulations and the market crab fishery. Outdoor Calif. 26(9):7-8.

Rauch, H. E., L. W. Botsford, and R. Shleser.
1975. The use of estimation theory to predict the growth of crabs and lobster. Proc. Fifth Symposium on Non-linear Estimation Theory and Its Applications, p. 208-216.

Ricker, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.

NET FEEDING IN MESOPELAGIC FISHES

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ABSTRACT

In an investigation of net feeding, 11 species of fish (5 gonostomatids, 6 myctophids) captured in a double-net Tucker trawl were examined. Stomach contents of fish retained by a coarse mesh "fish-catcher" in one net were compared to contents of fish which had accumulated with plankton in the cod end of the adjacent net. Out of 19 species-collection pairs (700 fish), there were significant ($P<0.05$) differences in number of prey items in stomachs of only three species in five collections. Two pairs, fish from the cod end and in three pairs, those from the "fish-catcher," contained significantly more prey than fish from the adjacent trawl. There were little or no significant differences between trawls in number of fish scales, prey diversity, or prey size. These results suggest that literature data on diet of mesopelagic fishes is not heavily biased from net feeding and that existing collections can be used for feeding investigations.

Diet studies of mesopelagic fishes taken from plankton net cod ends of mid-water trawls could be seriously biased if fish feed extensively in the cod end. Indirect evidence for net feeding in pelagic shrimp has been presented by Judkins and Fleminger (1972) and in myctophid fish by Anderson (1967). DeWitt and Hopkins (in press) also suggest the possibility of net feeding in *Pleuragramma antarcticum*, a mid-water notothenioid fish. The problem of net feeding, though recognized by the above authors and others (e.g., Holton 1969; Collard 1970; Hopkins and Baird 1973), is largely unresolved; consequently the validity of published data on the diet of mesopelagic fishes is questionable. The present study was initiated to estimate the nature and degree of net feeding in the cod end of plankton net trawls by mid-water fishes to better judge the reliability of published information on diets of these fishes, and to determine if existing collections and present methods of collecting are adequate for trophic studies.

METHODS

Most of the material examined was collected from the eastern Gulf of Mexico with a double (side-by-side) closing Tucker trawl (Figure 1). One side of the trawl had an unmodified plankton net at the cod end. The mouth of the cod end plankton net of the adjacent trawl was fitted with a coarse mesh (1.1 cm stretched) conical "fish-catcher." In principal, the conventional trawl allowed the passage of fish into the cod end where plankton was concentrated; in the adjacent trawl fish were prevented from accumulating with plankton in the cod end by the fish-catcher. The body of the trawl was constructed of 1.1-cm stretched, knotless mesh. The cod ends for most collections were 333-μm mesh, 0.5-m diameter plankton nets. In collections subsequent to tow 152 (see Table 1), 1,050-μm mesh nets were substituted for the finer 333-μm mesh cod ends to improve the internal flow characteristics of the trawl. Other details of trawl design are in Hopkins et al. (1973). We have also included data from tow 98, a Caribbean sample, made with a single-net closing Tucker trawl (Hopkins et al. 1973). Fish gilled in the body of the trawl in this tow were compared with specimens from the cod end. Trawl hauls represented discrete depth samples which ranged from horizontal tows (±10 m) to stepped oblique tows which sampled over a specified segment of the water column.

Fish were preserved in 10% Formalin[2] and subsequently transferred to 40% isopropyl alcohol. Specimens selected for analysis (370 from cod end; 332 from fish-catcher) were measured to the nearest millimeter (standard length, SL) prior to stomach removal. Contents of the pigmented distensible region posterior to the esophagus and anterior to the intestine were identified to genus when possible, measured, and counted (see Hopkins and Baird 1973; Baird et al. 1975). Prey

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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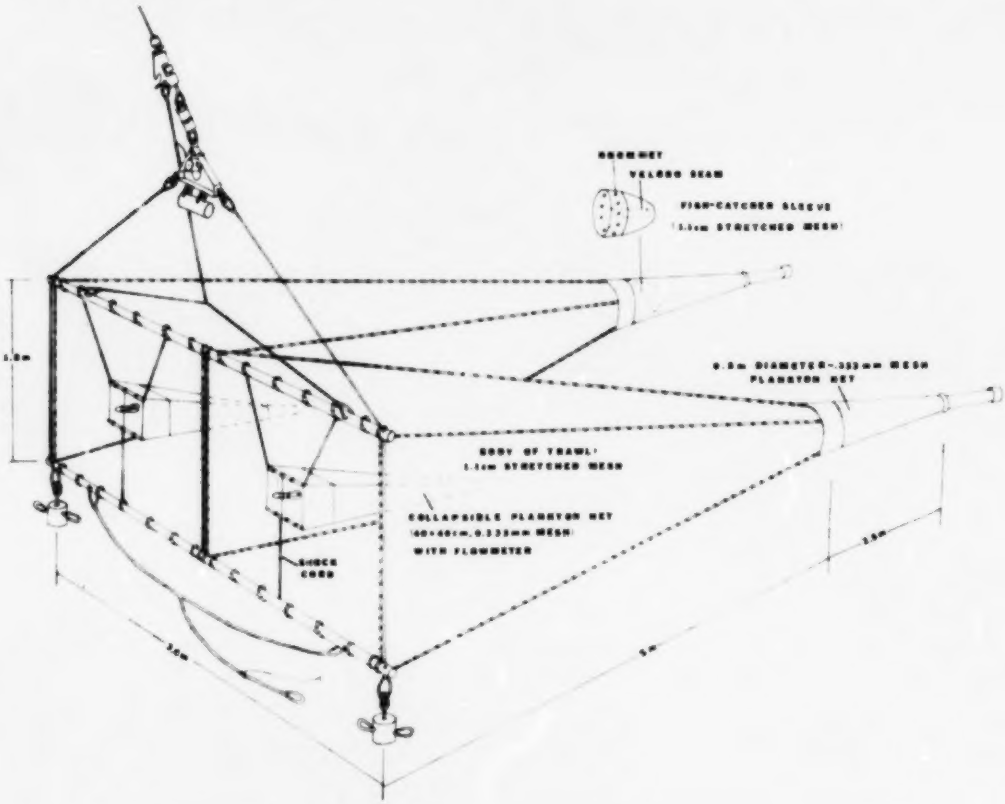

FIGURE 1.–Double-net closing Tucker trawl showing modified (fish-catcher sleeve) and conventional cod ends.

items contained in the mouth, pharyngeal region, esophagus, or intestine were not included in the analysis. Student's *t*-test was used for most statistical comparisons, the distributions being first tested for skewness and kurtosis (Sokal and Rohlf 1969). If the data to be tested were not normally distributed, then a log or square root transform was applied and the resulting distributions retested for skewness and kurtosis. *F*-tests were used to determine homogeneity of variances; the few exceptions to homogeneity will be discussed under the appropriate section. Standard chi-square tests were used to test the similarity of prey size distributions.

To compare prey availability in the trawl cod end with fish stomach contents, plankton was examined from tows 135, 137, and 141-144 (Table 2). Trawl mouth plankton net collections were used in preference to cod end catches because of possible losses of small plankton incurred in sorting larger fish and shrimp from the latter. Both cod end and trawl mouth nets for these particular tows had the same mouth area ($0.2\ m^2$) and mesh size ($333\ \mu m$) and were considered comparable in fishing characteristics, at least for the smaller plankton typically found in fish stomachs. Trawl mouth plankton collections for tow 137 were not available, consequently the catch from the cod end net of the fish-catcher side of the trawl was substituted. This particular cod end collection had not been "rough sorted" for larger organisms and was in excellent condition.

Zooplankton was identified, usually to genus, and counted in each of two subsamples. One plankton net collection (two subsamples) was analyzed for tows 135, 137, and 142 while two collections (four subsamples) were examined for the remaining tows. The mean number of

TABLE 1.–Comparison of diet characteristics of fish examined in net feeding investigation. F = "fish-catcher" side of double trawl; P = unmodified side of double trawl (see Figure 1); G = gilled in meshes of body of trawl; *t*-tests: * = $P<0.05$, ** = $P<0.025$, *** = $P<0.01$, **** = $P<0.005$.

Species	Trawl no.	Depth (m)	Time of collection	Trawl side	No. fish	Fish size (mm) $\bar{x}$ (range)	Prey items per stomach $\bar{x}$ (range)	Prey size (mm) $\bar{x}$	Prey diversity (taxa)	No. fish scales[2]
			Night (post-midnight)[1]							
Argyropelecus aculeatus	144	156-197	0220-0515	F	6	29 (24-36)	2.8 (0-8)	2.7	5	0
				P	8	31 (22-38)	6.4 (1-14)	3.7	15	2
Benthosema suborbitale	137	94	0227-0543	F	27	28 (23-31)	3.0 (0-7)	1.9	17	0
				P	25	28 (25-33)	3.5 (0-15)	2.0	20	6
Ceratoscopelus warmingi	137	94	0227-0543	F	25	33 (28-52)	8.5 (2-18)	1.8	42	0
				P	25	32 (28-48)	10.1 (1-28)	1.8	52	2
Gonostoma elongatum	144	156-197	0220-0515	F	23	96 (71-113)	2.7 (0-7)	6.2		
				P	29	97 (68-117)	2.0* (0-5)	5.4		
Lampanyctus alatus	141	128	0240-0350	F	32	39 (29-46)	5.8 (0-13)	2.9	26	1
				P	32	39 (28-45)	7.3*** (1-17)	3.2	39	7
Lepidophanes guentheri	137	94	0227-0543	F	36	50 (38-58)	6.6 (0-19)	4.0	31	9
				P	35	50 (37-58)	7.2 (0-17)	3.0	35	3
Notolychnus valdivae	141	128	0240-0350	F	10	20 (17-22)	2.7 (0-6)	2.9		
				P	39	20 (16-23)	2.6 (0-9)	2.5		
Valenciennellus tripunctulatus	152	397-450	0140-0545	F	8	28 (25-31)	2.3 (0-5)	2.7	6	0
				P	6	28 (25-32)	2.8 (2-4)	2.9	5	0
			Night (pre-midnight)							
Ceratosropelus warmingi	161	90-130	2047-2321	F	20	38 (32-45)	5.5 (0-13)	2.3		
				P	13	34* (29-45)	3.5**** (0-7)	2.3		
Diaphus dumerili	173	30-130	2108-2355	F	6	51 (37-66)	17.7 (7-29)	3.7	22	0
				P	6	48 (41-63)	11.3 (2-22)	4.1	17	0
Cyclothone pallida	147	781-844	2130-0100	F	23	44 (33-52)	0	0	0	0
				P	24	43 (28-52)	0.04 (0-1)	4.5	1	0
Lampanyctus alatus	167	60-130	2102-2350	F	30	41 (34-48)	3.2 (0-9)	3.9		
				P	24	38 (29-48)	4.8* (0-16)	4.2		
Lepidophanes guenthori	167	60-130	2102-2350	F	7	55 (48-59)	9.7 (3-19)	4.4	12	1
				P	7	33 (44-59)	11.7 (2-46)	5.2	12	0
Valenciennellus tripunctulatus	143	257-348	2117-2352	F	6	24 (23-27)	10.2 (3-16)	1.8		
				P	24	24 (21-29)	10.3 (0-23)	1.7		
			Day (morning)							
Argyropelecus hemigymnus	142	363-545	0920-1240	F	18	23 (17-29)	4.2 (0-11)	1.8		
				P	11	26 (19-33)	5.2 (0-11)	1.7		
Gonostoma elongatum	145	660-1,000	0830-1130	F	12	108 (93-120)	3.0 (1-5)	6.6	8	0
				P	10	110 (99-130)	1.3* (0-4)	4.2	6	0
Lepidophanes guentheri	98	570-705	0755-1112	F	15	48 (38-54)	9.1 (0-22)	4.1		
				G	19	49 (39-62)	9.3 (1-27)	3.7		
Valenciennellus tripunctulatus	142	363-545	0920-1240	F	19	27 (21-30)	3.7 (0-11)	2.1	12	0
				P	22	27 (24-31)	3.8 (9-10)	2.2	12	0
			Day (afternoon)							
Valenciennellus tripunctulatus	135	340-627	1435-1830	F	9	25 (21-29)	10.9 (0-16)	2.4	14	0
				P	11	24 (18-28)	11.5 (2-24)	2.0	13	0

[1] Time of tow initiation.

[2] Fish scales only; no other fish remains present.

plankters counted in each subsample was 775 (range: 453-1,079).

RESULTS

Fish Size Distribution

Because of possible relationships between number of items in stomachs (also other diet characteristics) and size of predator (e.g., Nesis 1965; Hopkins and Baird 1973), the mean length and size range of fish from each trawl were compared for each pair (Table 1). There were no significant differences in mean length (*t*-test, $P>0.05$) in 18 of 19 pairs. For the single exception, *Ceratoscopelus warmingi* from tow 161, the mean size of fish from the catcher size was larger ($P<0.05$; $\bar{x}$ (SL): 38 vs. 34 mm). However, since the distributions had considerable overlap, this set was included in the study.

Prey Abundance in Stomachs

It was necessary to apply a square root transform ($\sqrt{X+0.5}$) to the data on number of prey per stomach since the high frequency of empty

TABLE 2.–Relative abundance of principal (top 3) food items in fish stomachs and in plankton taken concurrently with fish, with 333-μm mesh nets mounted in the mouth of the double trawl (see Figure 1): F = "fish-catcher" set of fish; P = cod end plankton net set.

Species	Tow	Top 3 prey items in stomachs	Numerical abundance of prey in stomachs (%)			Numerical abundance in plankton nets (%)	Top 3 items in plankton nets	Numerical abundance in plankton nets (%)
			F	P	$\bar{x}$			
Argyropelecus hemigymnus	142	*Oncaea*	45	42	43.5	12	*Eucalanus*	41
		Conchoecinae	17	23	20.0	5	*Oncaea*	12
		Eucalanus	12	9	10.5	41	Scolecithricidae	10
Benthosema suborbitale	137	*Oncaea*	23	24	23.5	9	Conchoecinae	12
		Pleuromamma	21	17	19.0	9	*Pleuromamma*	9
		Conchoecinae	11	10	10.5	12	*Clausocalanus*	9
Ceratoscopelus warmingi	137	*Limacina*	13	17	15.0	3	Conchoecinae	12
		Conchoecinae	12	14	13.0	12	*Pleuromamma*	9
		Siphonophores	12	11	11.5	2	*Clausocalanus*	9
Gonostoma elongatum	144	*Stylocheiron*	16	21	18.5	2	*Sagitta*	19
		Pleuromamma	13	33	23.0	1	Conchoecinae	18
		Conchoecinae	13	9	11.0	21	*Oithona*	14
Lampanyctus alatus	141	*Pleuromamma*	23	25	24.0	4	*Oithona*	14
		Stylocheiron	16	13	14.5	4	*Sagitta*	8
		Conchoecinae	8	6	7.0	8	Conchoecinae	8
Lepidophanes guentheri	137	*Pleuromamma*	25	31	28.0	9	Conchoecinae	12
		Euphausia	14	6	10.0	<1	*Pleuromamma*	9
		Conchoecinae	11	9	10.0	12	*Clausocalanus*	9
Valenciennellus tripunctulatus	142	*Oncaea*	24	12	18.0	12	*Eucalanus*	41
		Pleuromamma	19	22	20.5	3	*Oncaea*	12
		Eucheata	10	(6)	8.0	1	Scolecithricidae	10
		Eucalanus	(3)	15	9.0	41		
Valenciennellus tripunctulatus	143	*Oncaea*	40	38	39.0	9	*Pleuromamma*	15
		Pleuromamma	23	25	24.0	15	Conchoecinae	14
		Conchoecinae	6	8	7.0	14	*Oithona*	10
Valenciennellus tripunctulatus	135	*Eucalanus*	19	16	17.5	20	*Pleuromamma*	23
		Pleuromamma	16	14	15.0	24	*Eucalanus*	20
		Eucheata	10	(9)	9.5	<1	*Euphausia*	7
		Oncaea	(3)	19	11.0	1		

stomachs resulted in significant skewness in the distributions of many untransformed data sets. In three set comparisons there were significant differences (F-tests, $0.05 > P > 0.025$) in variance (*Benthosema suborbitale*, tow 137; *C. warmingi*, tow 137; *Lampanyctus alatus*, tow 167). In these cases, tests comparing means of normal distributions when population variances are unequal were applied as described by Johnson and Leone (1964:226).

There were significant (t-tests, $P < 0.05$) differences in 5 of 19 comparisons of number of prey items per stomach. *Lampanyctus alatus* in two collections contained more prey items per individual in fish taken from the plankton net cod end (tow 141: $0.025 > P > 0.01$; tow 167: $0.05 > P > 0.025$). However, for *Gonostoma elongatum* in two sets (tows 144, 145: $0.05 > P > 0.025$), and *C. warmingi* in one set (tow 161: $P < 0.005$), individuals from the fish-catcher side averaged more prey per stomach. Because of possible diurnal feeding periodicity in mid-water fishes (Anderson 1967; Holton 1969; DeWitt and Cailliet 1972; Baird et al. 1975), fish entering the trawl at different periods in their feeding cycle may be satiated or have a different predisposition to feed in varying degrees. The five sets of fish showing significant differences in number of food items, however, are not conspicuously grouped in any single time period (see Table 1) and no general relationship is apparent in our results between time of capture and relative abundance of prey in fish from either side of the trawl.

Mean Prey Size

In 8 of 19 data sets, mean prey size was smaller in cod end fish. The major size modes were coincidental in all 19 set comparisons as judged from visual inspection. A t-test of the grand means (mean of 19 individual means for each cod end type), however, revealed no significant ($P > 0.05$) difference in mean size of food item for fishes in either side of the trawl (variance of means homogeneous). Though the sensitivity of this test is weakened to some degree by comparing different species of fish collected at different times, a strong bias in prey size resulting from net feeding is not apparent.

Prey size distributions for 14 paired sets were also compared using the contingency chi-square test. Significant ($P < 0.05$) differences were found in only two pairs: *Lepidophanes guentheri*, tow 167 ($P<0.001$) and *Valenciennellus tripunctulatus*, tow 135 ($0.005>P>0.001$). In the former, those individuals from the cod end took more prey items in smaller size classes while in the latter the reverse occurred. We have no simple explanation for these results. It is difficult to attribute them, however, to net feeding since other diet characteristics tested showed no significant differences for these same sets. Additionally, paired samples of the same species from other collections revealed no significant differences.

Prey Diversity

In comparison to the coarse mesh fish-catcher, the unobstructed cod end net of the adjacent trawl contained a much greater variety of plankton and consequently a more diverse potential food source for net feeding. A comparison was made of diversity of food items in stomachs of fish from each side of the trawl using 12 (of 19) species-pair collections represented by sets of approximately equal numbers of individuals for each cod end type. Total diversity was scored for each set of fishes, yielding two diversity values for each species-pair collection. Diversity scores were then summed to give grand means for each cod end type.

On the basis of a t-test on $\log_{10}$ transformed data, no significant ($P>0.05$) difference was indicated for the two cod end types though total diversity was considerably greater in fishes from the plankton net cod end in some sets (e.g., *Argyropelecus aculeatus*, tow 144; *L. alatus*, tow 141).

Fish Scales

Anderson (1967), in his analysis of the diet of *Bathylagus stilbius*, frequently encountered fish scales in stomachs yet no other remains of fish of the size indicated by the scales. This, in addition to the absence of scales in intestines and the occurrence of scales and copepods in the mouths of fish, he considered as evidence of net feeding. In the present study, fish in half the sets of samples (6 of 12) for which data are presented contained no fish scales. In four of the remaining six pairs, more scales were found in fish from the cod end where scales would be expected to accumulate during the course of a tow, but none of the differences were significant (t-test on $\sqrt{X+0.5}$ transformed data; $P>0.05$).

The occurrence of fish scales in stomachs does not necessarily stem from predation on smaller fish or from eating scales abraded from fish within the trawl. Fish scales appear to be common in the water column and thus available as separate forage items. In a series of paired 30-liter bottle casts made between 0 and 1,000 m in August 1972, in the eastern Gulf of Mexico where most of the fish examined were taken, scales occurred in collections (60 liters/sample) from 7 of 15 depths sampled at densities of 17-83 per m^3. Scales ranged from 0.5 to 5 mm in diameter. No fish were taken in the sample bottles and the probability of contamination from other sources appears low.

Taxonomic Composition of Stomach Contents and Plankton

Table 2 presents the principal taxonomic components of prey found in nine sets of fish from both sides of the trawl. The principal diet item was the same in both sets of fish in six of nine collections, the same prey constituted the top three food items by number in seven of nine collections and the prey taxa were in the same rank order in five of nine collections. The principal three prey taxa in fish from either side of the trawl were within ±3% of the mean value for both sides from each tow in 25 of 29 food item comparisons and all values were within ±10% of the means. These results show that the taxonomic composition of at least the principal components of the diet was similar in fish from both sides of the trawl for all comparisons.

Comparison of food items in stomachs of fish from the cod end, where net feeding is assumed mostly likely to occur, with plankton catches reveals little similarity in the top three taxonomic components. In none of the nine collections was the principal taxon the same in either the plankton net catch or in the stomachs of fish from the cod end. Of particular importance are tows 137, 141, 144, 152, and 161 which sampled relatively narrow depth zones and consequently were potentially less influenced by vertical stratification of plankton. Also, three species of fish collected in the same haul (tow 137) each contained a different principal food item, none of which matched the most abundant taxon in the cod end plankton catch. The major diet components for *Benthosema suborbitale*, *C. warmingi*, and *L. guentheri* from tow 137 were *Oncaea*, *Limacina*, and *Pleuromamma*; the most abundant plankton in the cod end net were ostracods (Conchoecinae). This particular haul was a horizontal tow in which a discrete depth was maintained throughout.

DISCUSSION

While studies of the behavior of mesopelagic fishes in small mid-water trawls used for research are nonexistent, there is considerable information available on fish behavior in larger commercial trawls of many kinds (e.g., Ben-Tuvia and Dickson 1968). Generally, fish move in front of or away from the walls of the trawl until they are exhausted and are collected in the cod end. Mesopelagic fishes from trawl cod ends often show signs of abrasion (Harrisson 1967); consequently, the likelihood of active and extensive net feeding would appear low. Several authors (e.g., Collard 1970; Hopkins and Baird 1973) have suggested that trauma induced by stress conditions in the trawl environment would operate against active feeding behavior. Reflexive gulping or "pseudo" feeding behavior, however, resulting in the ingestion of significant amounts of prey from the plankton rich cod end is a potential mechanism whereby stomach contents could be biased by net feeding. Several studies have revealed diel periodicity in feeding in mid-water fishes which indicates that at certain times, at least, net feeding cannot be extensive (Holton 1969; DeWitt and Cailliet 1972; Baird et al. 1975).

The possibility of fishes foraging in front of the cod end or fish-catcher can also be evaluated. At standard trawling speeds (3.7-4.6 km/h) the trawl moves at a rate of 1.0 to 1.3 m/s. For those epipelagic species which have been examined, foraging and cruising speeds range from about 1 to 4 body lengths per second and maximum burst speeds are on the order of 10 to 30 body lengths per second (e.g., Blaxter 1969; Baird et al. 1975). Assuming similar swimming capabilities for mid-water fishes and a fish size of 3 inches (76 mm), a conservative estimate of foraging speeds should be less than 0.3 m/s and burst rates of 0.8 to 2.3 m/s. All of the species examined here were less than 76 mm in length except *G. elongatum* which may have somewhat limited swimming capabilities (Marshall 1971). In view of the swimming speeds required, extensive foraging in front of the cod end appears remote. In addition, the data from *L. guentheri* (tow 98), where prey of individuals gilled in the net were compared with those from the cod end, failed to reveal indications of net feeding.

The present results support the contention that if net feeding does occur, it is not extensive in the relatively small fragile fishes typical of the oceanic mesopelagic enrivonment. Only the data on prey abundance in stomachs of *L. alatus* could be construed as statistical evidence of net feeding. In both of these collections, however, mean size of prey items and taxonomic composition of diet were very similar in both sets of fish, while the diet showed little agreement in terms of principal taxonomic components (Table 2) with plankton in the cod end, as might be expected from net feeding. In three collections (tows 144, 145, 167), *G. elongatum* (2 sets) and *C. warmingi* (1 set) from the "control" side contained more food items than fish from the cod end. Here again comparisons of mean prey size, taxonomic composition of diet, and major taxa in diet with that in cod end plankton samples failed to reveal evidence of net feeding. Furthermore, there were often substantial differences between principal taxonomic components of diet and plankton from cod end catches from the same haul. Mean prey size (with two exceptions) and composition of principal taxa of diets were nearly identical for all sets of comparison which further indicate the limited nature of net feeding in this study.

The use of fish scales as a criterion for net feeding poses a number of difficult problems. Our hydrocasts reveal, for instance, that fish scales occur naturally in the water column. Further, several studies of both marine and freshwater teleost fishes have shown that scales (probably also the covering mucous and epidermis) can serve as a major component of the diet, appear to be easily digested, and may possibly have considerable nutritive value (e.g., Roberts 1970, 1973; Carr and Adams 1972, 1973). Scales were relatively rare in stomachs examined here but did occur in fishes from both sides of the trawl. Since scales are present in the natural environment, may have nutritive value, and are possibly easily seen, captured, and eaten, they could serve as a natural food source or provide appropriate stimuli to elicit ingestion. Until more evidence is obtained concerning the role of scales in the natural diets of fishes and their abundance in oceanic environments, the presence of scales in the stomachs of mid-water fishes cannot be used with assurance as an indicator of net feeding.

Because of the difficulty of replicating trawl conditions and obtaining sufficient material for analysis, the variability in distributions of mid-water fishes with respect to time and space, and possible variations in feeding cycles, the present collections are not ideal in all respects. The study did include representatives of most of the major groups of common mesopelagic fishes from a variety of depths and times, and the results may be expected to be broadly applicable to many midwater environments. Considering the simultaneous time-depth collections with the double trawl of both "control" fish and those with the opportunity to ingest food in the cod end, this study provides the first reasonably good test of net feeding in mesopelagic fishes. The relatively small differences in the mean number and taxonomic composition of prey items in most sets of stomachs are encouraging. The results presented here suggest that the published literature on the diets of mesopelagic fishes is not seriously biased by net feeding and that existing collections can be used for trophic investigations.

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LITERATURE CITED

Anderson, R.
1967. Feeding chronology in two deep-sea fishes off California. M.S. Thesis, Univ. South California, Los Ang., 22 p.

Baird, R. C., T. L. Hopkins, and D. F. Wilson.
1975. Feeding chronology of *Diaphus taaningi* Norman in the Cariaco Trench. Copeia 1975:356-365.

Ben-Tuvia, A., and W. Dickson (Editors).
1968. Proceedings of the conference on fish behaviour in relation to fishing techniques and tactics. FAO (Food Agric. Organ. U.N.) Fish. Rep. 62:1-47.

Blaxter, J. H. S.
1969. Swimming speeds of fish. FAO (Food Agric. Organ. U.N.) Fish. Rep. 62:69-100.

Carr, W. E. S., and C. A. Adams.
1972. Food habits of juvenile marine fishes: Evidence of the cleaning habit in the leatherjacket, *Oligoplites saurus*, and the spottail pinfish, *Diplodus holbrooki*. Fish. Bull., U.S. 70:1111-1120.
1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Trans. Am. Fish. Soc. 102:511-540.

Collard, S. B.
1970. Forage of some eastern Pacific midwater fishes. Copeia 1970:348-354.

DeWitt, F. A., Jr., and G. M. Cailliet.
1972. Feeding habits of two bristlemouth fishes, *Cyclothone acclinidens* and *C. signata* (Gonostomatidae). Copeia 1972:868-871.

DeWitt, H. H., and T. L. Hopkins.
In press. Aspects of the diet of the Antarctic herring *Pleuragramma antarcticum* Boulenger. *In* G. A. Llano (editor), Third Symposium on Antarctic Biology: Adaptations within Antarctic Ecosystems.

Harrisson, C. M. H.
1967. On methods for sampling mesopelagic fishes. Symp. Zool. Soc. Lond. 19:71-126.

Holton, A. A.
1969. Feeding behavior of a vertically migrating lanternfish. Fac. Sci. 23:325-331

Hopkins, T. L., and R. C. Baird.
1973. Diet of the hatchetfish *Sternoptyx diaphana*. Mar. Biol. (Berl.) 21:34-46.

Hopkins, T. L., R. C. Baird, and D. M. Milliken.
1973. A messenger-operated closing trawl. Limnol. Oceanogr. 18:488-490.

Johnson, N. L., and F. C. Leone.
1964. Statistics and experimental design in engineering and the physical sciences, vol. 1. John Wiley & Sons, N.Y., 523 p.

Judkins, D. C., and A. Fleminger.
1972. Comparison of foregut contents of *Sergestes similis* obtained from net collections and albacore stomachs. Fish. Bull., U.S. 70:217-223.

[illegible]all, N. B.
1971. Explorations in the life of fishes. Harvard Univ. Press, Camb., Mass., 204 p.

Nesis, K. N.
1965. Distribution and feeding of young squids Gonatus fabricii (Licht.) in the Labrador Sea and the Norwegian Sea. Oceanology 5(1):102-108.

Roberts, T. R.
1970. Scale-eating American characoid fishes, with special reference to *Probolodus heterostomous*. Proc. Calif. Acad. Sci. 38:383-390.
1973. The glandulocaudine characoid fishes of the Guayas Basin in Western Ecuador. Bull. Mus. Comp. Zool. 144:489-514.

Sokal, R. R., and F. J. Rohlf.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.

NOTES

GAS-BUBBLE DISEASE: MORTALITIES OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN WATER WITH CONSTANT TOTAL GAS PRESSURE AND DIFFERENT OXYGEN-NITROGEN RATIOS[1]

A review of the literature regarding gas-bubble disease can be found in a recent publication by Rucker (1972); one by the National Academy of Science (Anonymous in press); and an unpublished report by Weitkamp and Katz (1973).[2] Most discussions on gas-bubble disease have dealt with the inert gas, nitrogen–oxygen was given a secondary role. It is important to know the relationship of nitrogen and oxygen when we are concerned with the total gas pressure in water. Where water becomes aerated at dams or falls, oxygen and nitrogen are usually about equally saturated, however, many of the samples analyzed from the Columbia River indicate that nitrogen is often about 7% higher than oxygen when expressed as a percentage. When oxygen is removed from water by metabolic and chemical action, or when oxygen is added to the water by photosynthesis, there is a definite change in the ratio of oxygen and the inert gases (mainly nitrogen with some argon, etc.). This present study shows the effect of varying the oxygen and nitrogen ratio in water on fingerling coho salmon, *Oncorhynchus kisutch*, while maintaining a constant total gas pressure.

The primary purpose of these experiments was to determine differences in lethality of various gas ratios of oxygen and nitrogen at a constant total gas pressure of 119%. I also wished to determine whether there was a difference in susceptibility between sizes and stocks of juvenile coho. Also to be examined was the effect of reducing the oxygen while holding the nitrogen constant.

Methods

Juvenile coho salmon averaging 6 cm in length, obtained from the Quilcene National Fish Hatchery, Quilcene, Wash., and the Northwest Fisheries Center of the National Marine Fisheries Service, NOAA (National Oceanic and Atmospheric Administration), Seattle, Wash., were used during all the tests concerning differences in lethality of O_2/N_2 ratios. During these tests water temperatures were 13.6° + 0.1°C. Gas concentrations usually varied slightly from the desired ratios. The tank facility consisted of six troughs, two of which were used to hold experimental fish at normal saturation (100%) and two pairs of troughs used to test fish at different gas ratios.

Control of gas concentrations and the test apparatus is described in a subsequent section. During initial testing of the gas control system, I determined that a ratio of 114% O_2 to 121% N_2 could be achieved by merely allowing air to be sucked into the intake side of the recirculation pump. Since this gas ratio did not require injection of either oxygen or nitrogen, the resultant concentration (114% O_2 and 121% N_2) was used as a quasi control for comparison with the other gas ratios. Several replicates were completed at this concentration. Water saturated at this ratio and concentration was also used to test for differences in size and stock and to provide base line data in determining effect of reduced oxygen concentrations while maintaining a constant nitrogen level.

In all the tests free carbon dioxide was near normal, or about 2 ppm. Oxygen is expressed as "O_2" and the inert gases as "N_2."

The number of days required to kill 25% of the fish at the different gas levels is expressed as the lethal exposure–LE_{25} and to kill 50% – LE_{50}.

Apparatus shown in Figure 1 was used to supply water with a definite oxygen and nitrogen content. The tank (1) was divided so that two experiments could be carried on simultaneously with similar equipment. Water was circulated by a centrifugal pump (2) with a valve (3) on the effluent side to cause a controlled back pressure as read on a gauge (4). This created a vacuum on the inflow side (5) so that air could be introduced into the water with either oxygen or nitrogen (6)

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[1] Research performed under contract with the U.S. Army Corps of Engineers.

[2] D. E. Weitkamp and M. Katz. 1973. Resource and literature review of dissolved gas supersaturation in relation to the Columbia and Snake River fishery resources. Submitted to Northwest Utilities Cooperative, c/o Idaho Power Co., Boise, Idaho, Apr. 3, 1973, by Seattle Marine Laboratories, Div. of Xelco Corp., Seattle, Wash., 55 p. (Typewritten.)

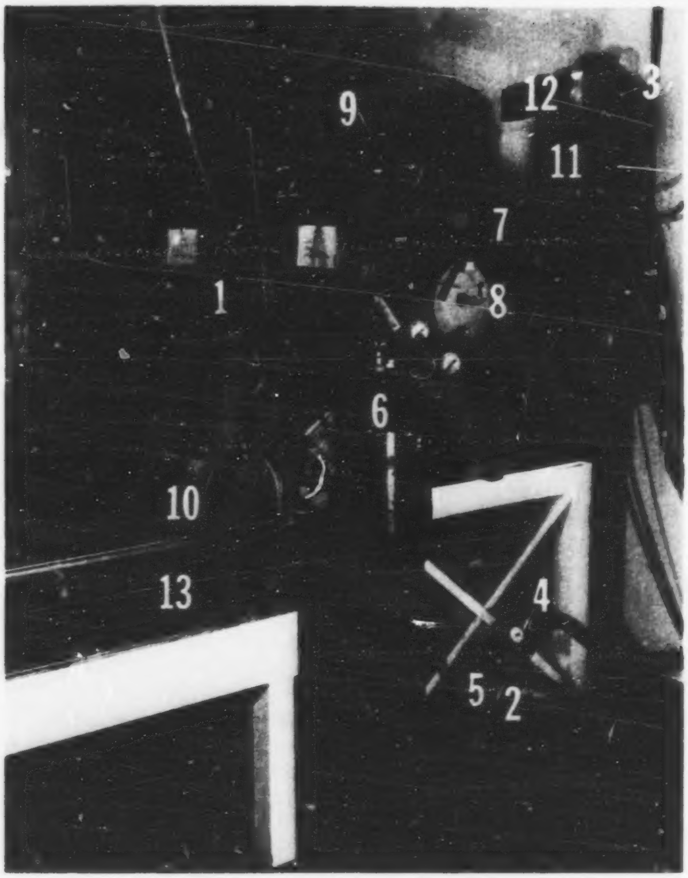

FIGURE 1.—Apparatus for subjecting fish to constant-temperature, flowing water with a definite oxygen and nitrogen content.

through a "Y" tube. Circulation of the water caused an increase in temperature which was maintained at approximately 13.6°C by means of a refrigeration system (7) and recorded on a thermograph (8). Water level in the tank was maintained by float valves (9). Each trough was supplied with 1 liter per minute of water regulated with flow meters (10). The water used was from the municipal supply, was soft, and was passed through activated charcoal to remove the chlorine. A greater depth of water was needed for absorption of the gases than was afforded by the tank (1), so two towers (11) were added to the system. The spout (12) at the top of the towers was to direct possible overflow water back into the system.

Inside dimensions of troughs in the fish holding area (13) were 104.5 × 23.5 × 20 cm high. Water depth was maintained at 14 cm. Each trough could be separated into three compartments with screens—"A" was at the inflow end of the trough, "B" middle, and "C" outflow end. In a few cases a compartment was divided longitudinally so that two groups of fish could be subjected to almost identical conditions.

Results

Effect of Variation in O_2/N_2 Ratios on Mortality

Times to death (LE$_{25}$ and LE$_{50}$) of juvenile coho salmon at various concentrations of O_2 and N_2 during constant total gas saturation of 119% appear in Table 1 are shown graphically in Figure 2. All tests were run in duplicate with 50 fish per test, except one at 229% O_2 and 90% N_2 which involve 50 fish but one test. With one exception (192% O_2 and

TABLE 1.–Time to death of groups of juvenile coho salmon (about 6 cm long) in 13.6°C water with total gas pressure of 119% of saturation and different ratios of O_2 and N_2.

Gas concentration (% saturation)		Time to death (days)			
		25% of all fish		30% c all fish	
O_2	N_2	Range	Average	Range	Average
50	138	1.8- 1.9	1.9	3.2-4.0	3.7
75	131	1.8- 2.7	2.3	3.5-4.3	3.9
114	121	3.2- 4.1	3.8	6.3-7.3	6.9
159	109	3.2- 5.3	4.5	6.5-9.1	8.2
173	105	33.5-35.3	34.4	—	(1)
192	100	—	[2]32.0	—	(3)
229	90	—	(4)	—	(4)

[1] Not reached, 28% mortality in 30 days.

[2] One replicate reached 24% mortality in 30 days; the other, 25% in 32 days.

[3] Not reached, test concluded at 33 days.

[4] Not reached, 20% mortality in 35 days.

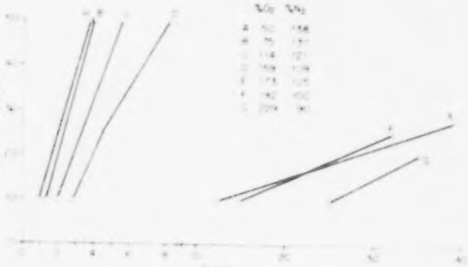

FIGURE 2.–Mortality pattern of 6-cm coho salmon reared at different O_2/N_2 levels at 13.6°C with a 119% total gas pressure.

100% N_2), all increases in ratio of O_2 to N_2 resulted in increased tolerance to the total gas saturation. A marked increase in tolerance to total gas pressure occurred between concentrations of 159%/109% and 173%/105% saturation of O_2 and N_2 (Figure 3).

Effect of Size and Stock of Fish on Mortality

A number of tests were carried out in the water containing 114% O_2 and 121% N_2 to determine effect of size and stock of fish on susceptibility to gas supersaturation (Table 2). Two groups of 3.8-cm coho from the Northwest Fisheries Center which had just started feeding were initially tested. One group of 96 fish reached LE_{25} in 22.9 days and LE_{50} after 30 days. The other group of 50 fish reached LE_{25} in 10.9 days. No further losses occurred until the 27th day. Loss at 30 days was 34%. Averages of the two groups placed LE_{25} at 16.9 days. Average loss at 30 days was 32%.

Two groups of 50, 4.6-cm fish from the Quilcene National Fish Hatchery were also tested. These tests produced LE_{25} of 15.1 and 18.3 days. LE_{50} was reached in 24.7 and 30 days. Averages of the above placed LE_{25} at 16.7 and LE_{50} at 27.4 days.

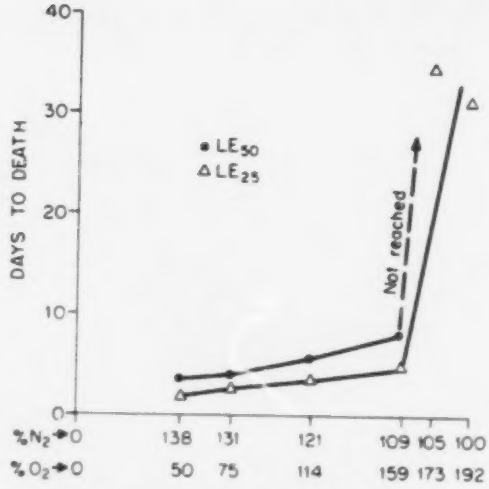

FIGURE 3.–Relationship between O_2/N_2 levels and time to death of 6-cm coho salmon fingerlings at 13.6°C and total gas concentration of 119%.

TABLE 2.–Time to death of groups of juvenile coho salmon of different body length and stock composition in 13.6° ± 0.1°C water with gas concentrations of 114% O_2 and 121% N_2.

Average body length and (in parentheses) stock of fish	Time to death (days)	
	25% of all fish	50% of all fish
3.8 cm (Seattle)	16.9	Not reached in 30 days
4.6 cm (Quilcene)	16.7	27.4
10 cm (Seattle)	2.1	2.6
10 cm (Quilcene)	2.9	4.2

Five groups of fish (8, 12, 16, 16, and 16 in number), and approximately 10 cm long, from the Northwest Fisheries Center were then tested. The average for all groups gave an LE_{25} of 2.1 days and an LE_{50} of 2.6 days.

Three groups of 12 fish each approximately 10 cm long from the Quilcene National Fish Hatchery were similarly tested. Averages were 2.9 days for LE_{25} and 4.2 days for LE_{50}.

These results indicate that the larger fingerlings approximately the same age are definitely more subject to harm from excess air in the water than the smaller fish. These data agree with those of Meekin and Turner (1974) and Dawley et al.[1]

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[1] E. Dawley, B. Monk, M. Schiewe, and F. Ossiander. 1974. Salmonid bioassay of supersaturation of dissolved gas in water. Northwest Fish Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., unpubl. manuscr.

Although the data are limited, there appears to be little difference between susceptibility of the Montlake and Quilcene stocks.

Effect of Reduced O_2 Concentration on Mortality

Fish held in compartments in a trough utilize oxygen so that the water in compartment C (outflow end) would have less oxygen than in compartment A (inflow end). Compartment B in the central part of the trough would have O_2 levels somewhere between those in A and C. Nitrogen levels in these compartments, however, were the same. To demonstrate the effect of reduced oxygen in relation to gas-bubble disease, 48 coho of 8.5 cm fork length were randomly distributed into compartments A, B, and C. Two additional replicates of the C compartment tests were run using 32 coho (8.5 cm) in each trial. These are listed as C_1 and C_2 in Table 3.

TABLE 3.–Time to death of groups of juvenile coho salmon (about 8.5 cm long) in 13.6°C water with 121% N_2 and different concentrations of O_2

Trough compartment	Gas concentration (% saturation)		Time to death (days)	
	O_2	Total pressure	25% of all fish	50% of all fish
A	113	119	2.5	3.3
B	110	118	3.6	5.3
C	105	117	3.8	5.3
C_1	105	117	4.2	6.6
C_2	105	117	5.4	6.6

Inspection of these data indicates that when 121% N_2 is maintained, oxygen plays a more significant role above 110% than below 110%.

Some of the data obtained when the oxygen-nitrogen ratio tests were done also illustrated the effect of reduced oxygen on the mortality rate. This was apparent in the experiment using 173% O_2 and 105% N_2. At 173% O_2 there were losses of 26 and 30% in 39 days, whereas slightly larger fish at the lower end of the troughs subjected to 169% O_2 had losses of only 7% in 39 days.

Pathology

Generally the fish died suddenly in the higher nitrogen concentrations. Never was tissue damage or any progressive pathology demonstrated. The fish always seemed to die from gas embolism, restricting the flow of blood through the gills. When the nitrogen was near normal and the oxygen high, the fish were moribund for many days before succumbing. These fish had blebs in the mouth which interfered with feeding and caused emaciation.

Summary

Coho salmon fingerlings were subjected to a total gas pressure of 119% at 13.6°C with the O_2/N_2 varying from 50%/138% to 229%/90%. The small fish (3.8 to 6 cm) were the most resistant and the larger fish (8 to 10 cm) the least resistant to gas-bubble disease at the gas concentrations used. A drastic decrease in lethal effect of individual ratios of O_2 to N_2 occurred between 159% O_2/109% N_2 and 173% O_2/105% N_2 at the same total gas pressure (119%).

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Literature Cited

ANONYMOUS.
In press. Total dissolved gases (supersaturation). *In* David Gates et al., Water quality criteria, p. 135-139. Natl. Acad. Sci.

MEEKING, T. K., AND B. K. TURNER.
1974. Tolerance of salmonid eggs, juveniles, and squawfish to supersaturated nitrogen. Wash. Dep. Fish., Tech. Rep. 12:78-126.

RUCKER, R. R.
1972. Gas-bubble disease of salmonids: a critical review. U.S. Fish Wildl. Serv., Bur. Sport Fish. Wildl. Tech. Pap. 58, 11 p.

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AGE-LENGTH-WEIGHT AND DISTRIBUTION OF ALASKA PLAICE, ROCK SOLE, AND YELLOWFIN SOLE COLLECTED FROM THE SOUTHEASTERN BERING SEA IN 1961

Japanese fishing companies explored the trawl fish resources of the eastern Bering Sea in 1929 and 1931. They began commercial fish meal production in 1933 and continued until 1937; a frozen fish operation was initiated in 1940 but was interrupted by World War II (Bourgois 1951).[1] In 1954, Japan resumed trawling in the eastern Bering Sea, again producing fish meal and frozen fish. The Soviet Union began sending bottom trawl fleets to the eastern Bering Sea in 1959, and combined annual catches of flatfishes (excluding Pacific halibut, *Hippoglossus stenolepis*) by Japan-USSR rose to a peak in 1961 when it exceeded 600,000 metric tons (Fadeev 1965). In the years following 1961, eastern Bering Sea flatfish catches by Japan decreased and in the period 1963-1970 have averaged less than 20% of the 456,890 metric tons caught in 1961 (International North Pacific Fisheries Commission 1973). Comparable Soviet data are not available.

Prior to intensive exploitation of eastern Bering Sea resources, there were two groups of surveys in which samples of flatfish were taken to assess the age-length structure of the population. One such series was conducted by the U.S. Fish and Wildlife Service in 1947-49 (King 1949; Ellson et al. 1950; Wigutoff and Carlson 1950). The other surveys were made 10 yr later by the Soviet Union (summarized by Moiseev 1965). Age-length determinations from flatfish samples collected in 1949 were reported by Mosher (1954); the Soviet collections of 1957-60 were studied by Fadeev (1963), Mineva (1964), and Shubnikov and Lisovenko (1964).

In July-August 1961, personnel of the Bureau of Commercial Fisheries (now National Marine Fisheries Service) conducted a trawl survey of the southeastern Bering Sea. This survey, although conducted principally to estimate the abundance of Alaska king crab, *Paralithodes* spp., provided an opportunity to sample several flatfish species. The purpose of the present report is to present biological information on the distribution, age, length, and weight by sex for three commercially important species of Bering Sea flatfish: yellowfin sole, *Limanda aspera* (Pallas); rock sole, *Lepidopsetta bilineata* (Ayres); and Alaska plaice, *Pleuronectes quadrituberculatus* Pallas.

Methods and Materials

Sample Collection

Otter trawl hauls of 1-h duration were made at 51 predesignated stations 20 nautical miles (37 km) apart (Figure 1). The trawling speed of the vessel was about 2.5 knots (4.6 km/h). The trawl was a 400-mesh, Eastern type, as described by Greenwood (1958). A 1.5-inch (3.8 cm) mesh liner was laced into the cod end to retain small specimens which might otherwise pass through the 3-inch (7.6 cm) meshes in that part of the trawl. At the completion of each haul, the catch was examined, and the weight of each major component was estimated. At five of the stations where one or more of the target species was abundant, samples of yellowfin sole, rock sole, and Alaska plaice was selected for length-weight-age determination. Specimens were measured to the nearest centimeter to obtain a representation of individuals throughout the available length range. Each fish to be retained was then frozen individually in a plastic bag which was sealed to prevent shrinkage and weight loss through dehydration.

At the laboratory, 3 mo after collection, the specimens were thawed, the total length (snout to longest rays of the tail fin) was measured, the weight recorded to the nearest gram, and sex determined from an examination of the gonads.

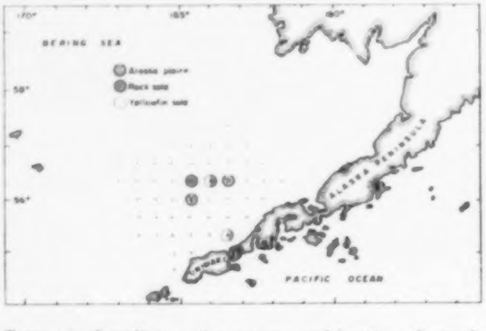

FIGURE 1.–Sampling station pattern and location of sample collections for 7 July-4 August 1961 survey.

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[1] Bourgois reported that Alaska pollock was the principal species taken by these Japanese fisheries. However, Alverson et al. (1964) pointed out that the areas of the eastern Bering Sea fished by Japanese trawlers from 1933 to 1941 were the same locations as post-World War II flounder fisheries, so there is reason to doubt the complete accuracy of Bourgois' information as to species.

Both otoliths were removed and placed in 95% ethyl alcohol.[2]

Age Determination Procedure

Studies by Hatanaka (1968) of yellowfin sole from the southeastern Bering Sea indicate that the translucent zone of an otolith is formed once a year during the winter months. In our readings on otoliths from all species, each translucent zone was considered an annular mark. The outermost edge of each otolith was also translucent except in the younger fish where there was evidence of some beginnings of opaque summer growth. Thus, the ages recorded are the number of translucent rings starting with the smallest observable and including the outermost. For example, a fish captured in July 1961 with 10 rings on its otolith was considered to have been spawned and hatched in 1951. Fadeev (1965), through gonad examination, stated that Bering Sea yellowfin sole spawn in June-August, Alaska plaice in April-June, and rock sole in February-May. Shubnikov and Lisovenko (1964), who reported that rock sole in Bristol Bay spawn in March-June, are in general agreement with Fadeev.

For reading, the otoliths were immersed in water in a petri dish with a black mat background and examined at 10× under reflected light with a dissecting microscope. Both otoliths were considered in age determination, but when a discrepancy occurred between the two otoliths, a decision was based on the eyed-side (right) otolith. In situations where the annular rings were not clear, the otoliths were ground on fine, water soaked, carborundum paper. In most samples grinding improved interpretation of annular rings, but the grinding of rock sole otoliths often exposed additional opaque and translucent zones to further confuse the readers.

Consistency of Age Determinations

Without reference to fish size, otoliths were interpreted by each author. A third, independent interpretation was made by an experienced otolith reader at the Northwest Fisheries Center. The observed ages, as agreed upon between the two authors, were compared with ages determined by the experienced reader. Initial agreement between authors and reader was 76% for yellowfin sole, 72% for Alaska plaice, and 85% for rock sole. Disagreements were not confined to a particular age class; only 3% differed by more than 1 yr, and these differences were equally negative and positive. The similarity of results by authors and reader suggests that the method used produced consistent age-growth data. Otolith interpretations not in agreement between the authors and the reader were reread and a joint decision was made on the most probable age of the fish.

Results and Discussion

Distribution

Yellowfin sole is the most abundant flatfish taken in the eastern Bering Sea. Alaska plaice (33% by weight of yellowfin sole caught) was usually encountered together with yellowfin sole and share a similar distribution within the sampling area (Figure 2). Fadeev (1970) and Maeda et al. (1967) note that yellowfin sole concentrate in the colder waters of Bristol Bay during the spring and summer months. In July of 1961, a tongue of cold water extended into the sampling area and the greatest concentrations of yellowfin sole and Alaska plaice were taken at bottom temperatures of 3°C or less.

The distribution of rock sole within the sampling area (28% by weight of yellowfin sole catch) was spotty with the denser concentrations occurring toward the eastern edge of the area inhabited by yellowfin sole and Alaska plaice. The 1961 observations are compatible with the contention of Shubnikov and Lisovenko (1964) that rock sole disperse during the summer into shallower water than they occupy in winter and spring.

Age-Length Observations

The age-length-weight composition for the three southeastern Bering Sea flatfish species sampled in 1961 are given in Tables 1-3.[3] It is difficult to compare the 1961 data with any earlier reports except in a generalized manner since in only one instance (Pruter and Alverson 1962) is there a determination of age by sex. The data presented in Tables 1-3, and also in studies of eas-

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[2] All otoliths from the 1961 collection are in permanent storage at the Northwest Fisheries Center, Seattle, Wash.

[3] Individual age determinations and related lengths and weights, by sex, are available upon request from the Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash.

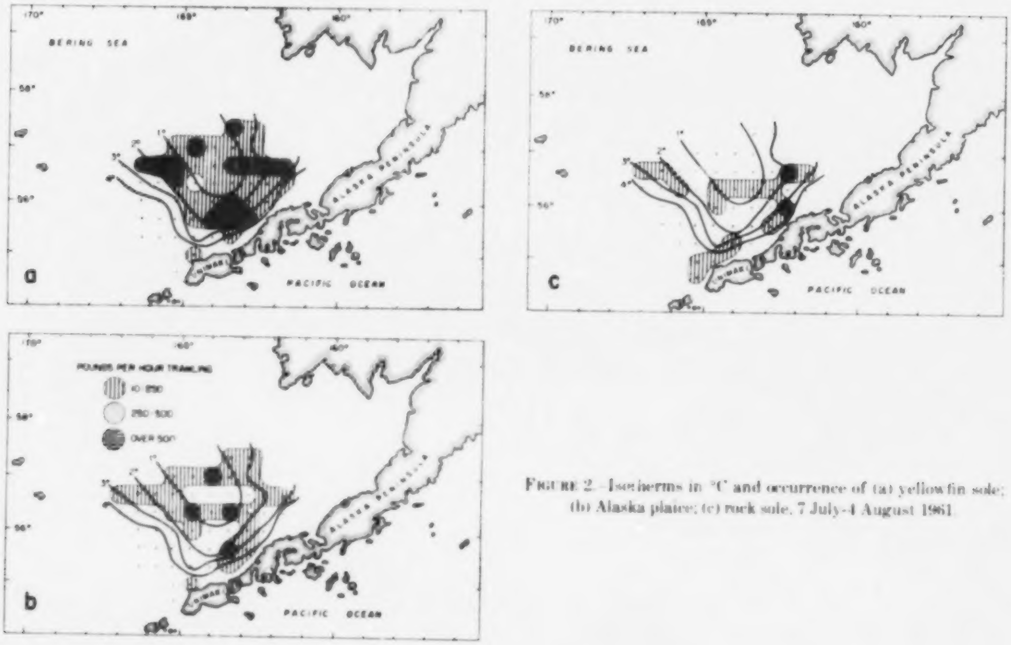

FIGURE 2.—Isotherms in °C and occurrence of (a) yellowfin sole; (b) Alaska plaice; (c) rock sole, 7 July-4 August 1961.

TABLE 1.—Observed age and length distribution of male (M) and female (F) yellowfin sole taken in the southeastern Bering Sea in 1961.

Length (cm)		4		5		6		7		8		9		10		11		12		13		Total		
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Total
17.5		1	1																			1	1	2
18.5					1			1														1	1	2
19.5				2	1	1		1			1	1										5	2	7
20.5						2		1	1	3	2	1										7	3	10
21.5					2	1		2	4	6	4	4										13	10	23
22.5				1	2	2	1	4	2	7	4	3										17	9	26
23.5								4	1	3	2											7	3	10
24.5						1		1		5	3			1	1							8	4	12
25.5							1	1		6	2	2	2				1					9	6	15
26.5										1	4	2		1								4	4	8
27.5									1	1	2	2	1	2	2			1				6	6	12
28.5									1	1		2	2	1	1	1						5	4	9
29.5											1		1		1		1		1				5	5
30.5													1					1				1	1	2
31.5																			2	1		1	2	3
32.5															2								2	2
33.5																	1		1				2	2
34.5																					1		1	1
Total		1	1	3	6	7	2	15	10	33	25	17	7	5	7	1	3	2	4	1	1	85	66	151
Average length[1]	(M)	18.0		20.6		21.8		22.5		23.6		24.3		27.2		28.5		28.9		32.0				
	(F)		17.3		21.2		23.9		23.3		24.2		28.0		29.1		30.0		31.6		34.8			
Average weight (g)	(M)	57		94		130		128		146		150		226		280		269		409				
	(F)		54		108		145		147		163		262		310		350		364		538			

[1] Calculated from ungrouped data.

tern Bering Sea yellowfin and rock sole by Hatanaka (1968), Maeda (1969), and Levings (1967), indicate that growth is different for each sex.

The ages of 12 yellowfin sole (10 female, 2 male) taken 50 miles south of Nunivak Island in the eastern Bering Sea in August 1959 (Pruter and Alverson 1962) fall within the range of our observations with some suggestion that the younger fish in their samples are slightly smaller. Maeda (1969) and Hatanaka (1968) derived age-length curves

TABLE 2.–Observed age and length distribution of male (M) and female (F) Alaska plaice taken in the southeastern Bering Sea in 1961.

Length (cm)	4		6		7		8		9		10		11		12		14		16		Total		
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Total
21.5		1																				1	1
22.5	1																				1		1
23.5																							
24.5																							
25.5	1																				1		1
26.5																							
27.5			1																		1		1
28.5			1																		1		1
29.5			1																		1		1
30.5			4	1					1												5	1	6
31.5									1				1	1							2	1	3
32.5			1	1	4	1			2		1	1	1								9	3	12
33.5			2	1		2	2			1			1								5	4	9
34.5			1		1	1	2	1	1		1		1	1							7	3	10
35.5						1	1	1	1			1	3			1					5	4	9
36.5								1	2		1	2									3	3	6
37.5				1				1					1	1		1					1	4	5
38.5										1		1	1		1						2	2	4
39.5										1		1						1		1		4	4
40.5												1		1								2	2
41.5										1						1						2	2
42.5										1				1								2	2
43.5										1												1	1
44.5																1						1	1
Total	2	1	11	4	5	5	5	4	8	6	3	7	9	5	1	4		1		1	44	38	[1]82
Average length[2] (M)	23.7		31.0		33.1		34.4		34.0		34.5		35.0		38.0								
(F)		21.5		33.7		33.9		36.4		40.0		37.2		37.3		40.1		40.0		39.5			
Average weight (g) (M)	188		384		438		484		503		531		538		690								
(F)		108		545		530		651		925		687		738		860		715		862			

[1] One additional male, age 18 yr, length 47.6 cm, 1,380 g.
[2] Calculated from ungrouped data.

TABLE 3.–Observed age and length distribution of male (M) and female (F) rock sole taken in the southeastern Bering Sea in 1961.

Length (cm)	4		6		7		8		9		10		11		Total		
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Total
18.5	1														1		1
19.5																	
20.5																	
21.5																	
22.5																	
23.5							1								1		1
24.5							1				1				2		2
25.5			2				2		2	1		1			6	2	8
26.5					3			2	6		5				14	2	16
27.5					1		1	2			2	1			4	3	7
28.5							1	2	2	2	1	4		1	4	9	13
29.5							1			2		3			1	5	6
30.5										2		3		1		6	6
31.5										1						1	1
32.5										1				2		3	3
33.5												1		1		2	2
34.5												1				1	1
Total	1		2		4		7	6	10	9	9	14		5	33	34	67
Average length[1] (M)	18.1		25.7		27.1		26.6		26.8		26.8						
(F)								27.6		29.8		29.9		31.8			
Average weight (g) (M)	55		198		217		216		212		219						
(F)								223		330		320		404			

[1] Calculated from ungrouped data.

from large samples of eastern Bering Sea yellowfin sole collected in 1963 and 1965-66, respectively. There is no appreciable difference between the two above age-length curves and our 1961 data (Figure 3).

With rock sole, the only comparative age-length data by sex is presented by Levings (1967) for samples collected in the northeastern Bering Sea in 1963. Levings' age-length observations on male rock sole are similar to our collections, but a considerable difference exists in female lengths-at-age. The females taken in 1963 are older and at a

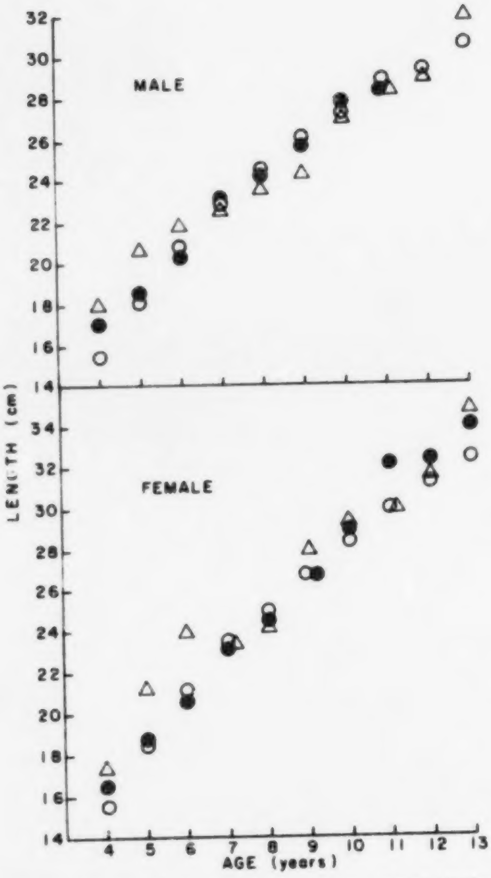

FIGURE 3.–Age-length comparison for yellowfin sole taken in the eastern Bering Sea in 1961 (open triangles); 1963 (closed circles, Maeda 1969); and 1965-66 (open circles, Hatanaka 1968).

comparable age average 10% greater in length (Figure 4).

No age-length information has been reported for Alaska plaice except that by Mosher (1954). The otolith observations by Mosher in 1949, though not separated by sex, indicate a markedly slower growth rate for younger fishes than that observed in our 1961 samples (Figure 5). Mosher (1954) comments that in his sample of Alaska plaice the first three to seven annular rings on each otolith were compressed and that beyond this zone, the annuli were farther apart. We noticed this same growth pattern in some of the otoliths from our collection, but it was not consistent.

In reflecting on the significance of similarities

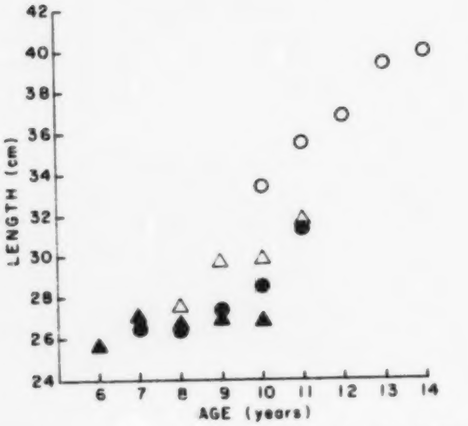

FIGURE 4.–Age-length comparison for rock sole taken in the eastern Bering Sea in 1961 (open triangles, female; closed triangles, male) and in [illegible] (open circles, female, closed circles, male; from [illegible]).

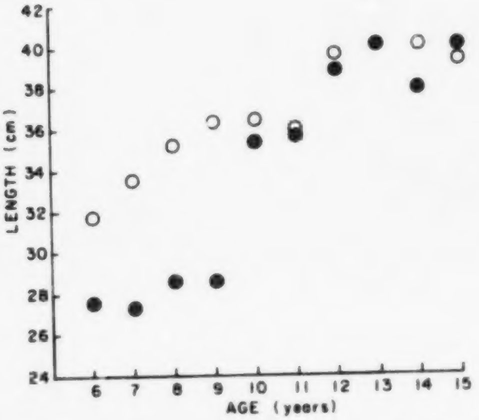

FIGURE 5.–Age-length composition (average length of combined sexes) for Alaska plaice taken in the eastern Bering Sea in 1949 (closed circles, from Mosher 1954) and 1961 (open circles).

or differences between our results and those obtained by other authors, we feel that a number of points should be considered. First, we recognize that our samples were collected from the southern part of the distribution of these species in the eastern Bering Sea, and some of the specimens with which we make comparisons were taken in another part of the range and may represent another population. It was determined by Fadeev (1970) that the yellowfin sole of the southeastern

Bering Sea do constitute a single population, but no such determinations have been made for rock sole and Alaska plaice. Second, there is no evidence of validity for the ages we obtained from otoliths; that is to say that we do not know how well the otolith ages represent the true age of the fish. Additionally, we must assume that otoliths were interpreted and recorded in essentially the same manner by all investigators.

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Literature Cited

ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT.
1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillian Lect. Fish., Inst. Fish., Univ. B.C., 190 p.

BOURGOIS, F.
1951. Japanese offshore trawling. U.S. Fish Wildl. Serv., Fish. Leafl. 389, 60 p.

ELLSON, J. G., D. E. POWELL, AND H. H. HILDEBRAND.
1950. Exploratory fishing expedition to the northern Bering Sea in June and July, 1949. U.S. Fish Wildl. Serv., Fish. Leafl. 369, 56 p.

FADEEV, N. S.
1963. Yellowfin sole of the eastern Bering Sea (a short biological description). Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 48 (Izv. Tikhookean. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 50):281-291. (Transl. in Soviet Fisheries Investigations in the Northeast Pacific, Part I, p. 297-307, by Israel Program Sci. Transl., 1968, available Natl. Tech. Inf. Serv., Springfield, VA, as TT 67-51203.)
1965. Comparative outline of the biology of flatfishes in the southeastern part of the Bering Sea and condition of their resources. Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 58 (Izv. Tikhookean. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 53):121-138. (Transl. in Soviet Fisheries Investigations in the Northeast Pacific, Part IV, p. 112-129, by Israel Program Sci. Transl., 1968, available Natl. Tech. Inf. Serv., Springfield, VA, as TT 67-51206.)
1970. The fishery and biological characteristics of yellowfin soles in the eastern part of the Bering Sea. Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 70 (Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 72):327-390. (Transl. in Soviet Fisheries Investigations in the Northeastern Pacific, Part V, p. 332-396, by Israel Program Sci. Transl., 1972, available Natl. Tech. Inf. Serv., Springfield, VA, as TT 71-50127.)

GREENWOOD, M. R.
1958. Bottom trawling explorations off southeastern Alaska, 1956-57. Commer. Fish. Rev. 20(12):9-21.

HATANAKA, H.
1968. Age and growth of yellowfin sole in the Southeastern Bering Sea. [In Jap., Engl. abstr.] Bull. Jap. Soc. Sci. Fish. 34:562-569.

INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION.
1973. Statistical yearbook 1971. Vancouver, B. C., 91 p.

KING, J. E.
1949. Experimental fishing trip to Bering Sea. U.S. Fish Wildl. Serv., Fish. Leafl. 330, 13 p.

LEVINGS, C. D.
1967. A comparison of the growth rates of the rock sole (*Lepidopsetta bilineata*) Ayres, in Northeast Pacific waters. Fish. Res. Board Can., Tech. Rep. 36, 43 p.

MAEDA, T.
1969. Studies on the trawl fishing grounds in the eastern Bering Sea—III. On the age and length compositions of yellow-fin sole. [In Jap., Engl. abstr.] Bull. Jap. Soc. Sci. Fish. 35:251-257.

MAEDA, T., T. FUJII, AND K. MASUDA.
1967. Studies on the trawl fishing grounds of the eastern Bering Sea—I. On the oceanographic condition and distribution of the fish shoals in 1963. [In Jap., Engl. abstr.] Bull. Jap. Soc. Sci. Fish. 33:713-720.

MINEVA, T. A.
1964. On the biology of some flatfishes in the eastern Bering Sea. Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 49 (Izv. Tikhookean. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 51):215-224. (Transl. in Soviet Fisheries Investigations in the Northeast Pacific, Part II, p. 227-235, by Israel Program Sci. Transl., 1968, available Natl. Tech. Inf. Serv., Springfield, VA, as TT 67-51204.)

MOISEEV, P. A.
1965. What research in the Bering Sea has demonstrated. Dal'ryba. Tsentral'noe Byuro Tekhnicheskoi Informatsii, Vladivost., 27 p. (Transl., 1966, available Lang. Serv. Div., Natl. Mar. Fish. Serv., Wash., D.C.)

MOSHER, K. H.
1954. Use of otoliths for determining the age of several fishes from the Bering Sea. J. Cons. 19:337-344.

PRUTER, A. T., AND D. L. ALVERSON.
1962. Abundance, distribution, and growth of flounders in the southeastern Chukchi Sea. J. Cons. 27:81-99.

SHUBNIKOV, D. A., AND L. A. LISOVENKO.
1964. Data on the biology of rock sole of the southeastern Bering Sea. Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 49 (Izv. Tikhookean. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 51):209-214. (Transl. in Soviet Fisheries Investigations in the Northeast Pacific, Part II, p. 220-226, by Israel Program Sci. Transl., 1968, available Natl. Tech. Inf. Serv., Springfield, VA, as TT 67-51204.)

WIGUTOFF, N. B., AND C. B. CARLSON.
1950. S.S. *Pacific Explorer* Part V. 1948 operations in the North Pacific and Bering Sea. U.S. Fish Wildl. Serv., Fish. Leafl. 361, 161 p.

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FURTHER STUDIES REGARDING EFFECTS OF TRANSPORTATION ON SURVIVAL AND HOMING OF SNAKE RIVER CHINOOK SALMON AND STEELHEAD TROUT

Losses to juvenile and adult Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, populations migrating in the Columbia and Snake rivers have increased dramatically in recent years. The principal migratory route over which most salmonids must pass has been artifically altered by construction of a series of dams. The dams, with their associated reservoirs, are a major source of mortality to migrating salmonids. Ebel et al. (1973) summarized the primary causes of mortality which include gas bubble disease, turbines at dams, and predation.

There is evidence that certain stocks of salmonids are in grave danger unless ways are found to increase their populations. For example, 1973 returns of summer-run chinook salmon, *O. tshawytscha*, to the Columbia and Snake rivers reached all-time low proportions. Other wild stocks of steelhead trout and chinook salmon also continue to decline.

The National Marine Fisheries Service conducted transportation experiments at Ice Harbor Dam during 1968-70 to find ways of increasing survival of Snake River salmonids.

In these experiments, juvenile salmon (spring- and summer-run chinook) and steelhead were collected at Ice Harbor Dam and transported to two locations downstream. Evaluation of these tests depended upon adults returning to Ice Harbor Dam and, subsequently, to their native streams. Data on adults returning from releases of juvenile chinook in 1968 and of juvenile steelhead in 1969 were analyzed and reported by Ebel et al. (1973). Analyses of adult returns from releases of juvenile chinook in 1969-70 and of juvenile steelhead in 1970 are covered in this addendum report.

Methods

General Procedures

Migrating juvenile chinook salmon (spring- and summer-run populations) and steelhead trout were collected at Ice Harbor Dam by dipnet from gatewells (Bentley and Raymond 1969) in 1969 and from a bypass collection area (Park and Farr 1972) at Ice Harbor Dam in 1970. Collection from the bypass area differed from dipnetting in that fish were accumulated in a holding area over a 24-h period. After accumulation, the fingerlings were raised by a fish pump about 15 m to an aerated tank truck for hauling to the fish marking facility. In both years populations were mixed and randomized before marking. The adipose fin was excised, a thermal brand (Mighell 1969) placed on the side of the fish, and a magnetic wire tag (Jefferts et al. 1963) injected into the snout of each fish. The control or nontransported group was released about 15 km above Ice Harbor Dam. The transported groups were released 5 km downstream from John Day Dam on the Oregon side of the Columbia River and 1 km downstream from Bonneville Dam on the Washington side of the river (Figure 1). Distinguishing brands and color-coded wire were assigned to each experimental group.

Numbers of juvenile chinook salmon and steelhead trout marked and released at various locations are shown in Table 1. In both 1969 and 1970, collection of juveniles fell below expectations. For example, we were able to mark only 28,956 chinook salmon in 1970. Therefore, numbers of marked returning adults were reduced accordingly.

Evaluation of Returning Adults

The effect of transportation of juveniles on their survival and homing as adult fish was evaluated by comparing recoveries of transported and nontransported adults at various sites in the river system as they returned on their spawning

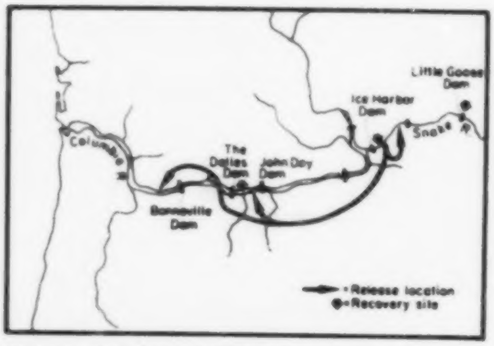

FIGURE 1.—Columbia and Snake rivers, showing release and recovery sites of migrating chinook salmon and steelhead trout.

Annual fish passage report Columbia River projects, 1973. North Pacific Division, U.S. Army Corps of Engineers, P.O. Box 2946, Portland, OR 97208.

TABLE 1.–Number of transported and nontransported (control) juvenile chinook salmon and steelhead trout that were marked and released, 1969-70 (figures adjusted for tag loss)[1].

Release site (experimental group of fish)	1969		1970	
	Chinook	Steelhead	Chinook	Steelhead
Ice Harbor Dam (control)	24,217	25,313	8,624	18,347
John Day Dam (transported)	14,782	20,430	10,159	20,935
Bonneville Dam (transported)	13,529	—	10,173	31,282
Total	52,528	45,743	28,956	70,564

[1] Initial tag loss was determined for the control releases by examination of juveniles after recovery at Ice Harbor Dam, 1969-70; tag loss for the test groups were determined by fish held at release sites after transport.

migration. These included returns to the sport, commercial, and Indian fisheries in the Lower Columbia River; to Ice Harbor and Little Goose dams on the Lower Snake River; to Rapid River and Dworshak hatcheries in Idaho; and to the spawning grounds.

Most of the tagged adults were captured at Ice Harbor Dam or Little Goose Dam. At Ice Harbor Dam about 80% of the run of adult fish ascend the south ladder enroute to the spawning grounds. At Little Goose Dam all fish must ascend the single ladder installed there. Adults were recovered at Ice Harbor Dam by a detector-separator device that intercepted tagged salmon and trout (Durkin et al. 1969). At Little Goose Dam, recoveries were made by an improved but similar detector apparatus. A major modification of the system included a Denil-type fishway instead of the pool-and-overfall ladder used at Ice Harbor Dam.[2] Improvements incorporated in the facility at Little Goose Dam increased detection efficiency markedly in 1970.

Results

Returns of Adult Spring and Summer Chinook to Ice Harbor and Little Goose Dams

Numbers of returning adult salmon successfully detected, separated, and identified at the adult separator are listed in Table 2. It should be stressed that the observed return of adults represents only a fraction of the total return of marked fish to Ice Harbor and Little Goose dams. The observed tally is low for the following reasons: 1) approximately 20% of the adult run at Ice Harbor Dam passed up the right bank (north) fishway which did not have a tag detection device; 2) at Little Goose Dam, the barrier gates at the entrance to the automatic separator were open at night (2100-0500) allowing some adults to pass undetected; 3) some tag loss had occurred between tagging and recovery as adults; 4) the tag detection system was less than 100% efficient; 5)

TABLE 2.–Percentage of transported and nontransported (control) juvenile chinook salmon (released in 1969 and 1970) that were recaptured as adults at Ice Harbor and Little Goose dams, 1 April through 18 August 1971-73.

Release site and (in parentheses) experimental group of fish	Number of juveniles released[1]	Number recaptured as adults	Percentage return as adults	
			Observed	Estimated[2]
1969:				
Ice Harbor Dam (control)	24,217	47	0.194	0.497
John Day Dam (transported)	14,782	19	0.129	0.356
Bonneville Dam (transported)	13,529	33	0.244	0.581
1970:				
Ice Harbor Dam (control)	8,624	17	0.197	0.323
John Day Dam (transported)	10,159	7	0.069	0.113
Bonneville Dam (transported)	10,173	29	0.285	0.467

[1] Adjusted for initial tag loss.

[2] Based on a comparison of the known recovery of fish with magnetized wire tags at Ice Harbor and Little Goose dams and the subsequent recovery of these and other marked fish at a hatchery upstream. Returning fish identified at the dam were marked with dart tags and released to continue their migration upstream. Numbers of dart-tagged fish arriving at Rapid River Hatchery were compared with the recovery of other wire-tagged fish not previously detected and identified at Ice Harbor and Little Goose dams.

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[2] Slatick E. 1974. Laboratory evaluation of a Denil-type steeppass fishway with various entrance and exit conditions for passage of adult salmonids and American shad. Unpubl. manuscr. Natl. Mar. Fish. Serv., NOAA, Pasco, Wash.

presumably some adults could have passed upstream through the navigation locks at Ice Harbor and Little Goose dams.

Throughout this section of the report, percentage figures are given which indicate either an increase or decrease in survival of groups of juveniles transported downstream in comparison to control groups not transported but released near the collection point. Some of the increases are statistically significant, some are not; generally those that are significant are indicated. We present the data even though some of it is not statistically significant because it parallels earlier data reported by Ebel et al. (1973).

The combined adult returns–of spring- and summer-run chinook salmon from juveniles transported from Ice Harbor Dam and, subsequently, released at Bonneville Dam–were greater than adult returns from control releases made at Ice Harbor Dam. The combined transportation benefit (Table 2) for spring- and summer-run chinook salmon released in 1969 was 27%; in 1970, 47%.

An analysis of comparative survival to adults for spring- and summer-run chinook salmon by year of transport are presented in Table 3. The transportation benefit indicated for juveniles released in 1969 was 27% for spring-run chinook salmon and 29% for summer-run chinook salmon. Benefits from the 1970 release were 40% for spring-run chinook salmon and 57% for summer-run chinook salmon.

Combined spring and summer adult returns from the John Day release were 34% less in 1969 and 65% less in 1970 than returns from the controls. Although the lower adult returns from juvenile releases at John Day are unexplained at this time, it is possible that the cumulative stress from collection, handling, and hauling combined with the stress from having to pass two dams (The Dalles Dam and Bonneville Dam) may have been detrimental for fish released at this site.

Returns of Adult Steelhead Trout to Ice Harbor and Little Goose Dams

Table 4 lists the returns of adult steelhead trout (released as juveniles in 1969-70) that were successfully detected, separated, and identified at the automatic separator at Ice Harbor and Little Goose dams. We identified 148 adult steelhead trout from those released in 1969. Of these, 46 were from the control release and 102 from the John Day transport release, which give a transportation benefit of 174%–a significant (X^2 = 34.370; df = 1) increase.

Adult steelhead trout returns from the 1970 juvenile releases totaled 324 fish. Of these, 71 were from the control release, 75 from the John Day transport release, and 178 from the Bonneville transport release. The transportation benefit from the Bonneville release was 47% (X^2 = 7.315; df = 1); however, no benefit was derived from transport of juveniles to the John Day release site (adult re-

TABLE 3.–Comparison between transported (released at Bonneville and John Day dams in 1969-70) and nontransported (control) groups of chinook salmon based on numbers of transported and nontransported juvenile fish recaptured as adults at Ice Harbor and Little Goose dams, 1971-73.

Release site (of juveniles) and seasonal race of salmon[1]	No. of salmon recaptured as adults at Ice Harbor and Little Goose dams[2]		Transportation benefit or deficit (−) (Percent)
	Transported	Nontransported	
1969			
Below Bonneville Dam:			
Spring chinook salmon	38	30	27
Summer chinook salmon	22	17	29
Below John Day Dam:			
Spring chinook salmon	23	30	−23
Summer chinook salmon	8	17	−53
1970			
Below Bonneville Dam:			
Spring chinook salmon	14	10	40
Summer chinook salmon	11	7	57
Below John Day Dam:			
Spring chinook salmon	4	10	−60
Summer chinook salmon	2	7	−71

[1] Seasonal races of chinook salmon in the Columbia River system are classified as spring, summer, or fall chinook depending on the time of year that the adults enter the river to spawn.

[2] Numbers recaptured adjusted in relation to numbers released (Table 1).

TABLE 4.–Percentage return and benefit or deficit (-) of transported to nontransported (control) juvenile steelhead trout (released in 1969-70) that were recaptured as adults at Ice Harbor and Little Goose dams, 1970-73.

Release site and (in parentheses) experimental group of fish	Number of juveniles released[1]	Number recaptured as adults				Percentage return as adults		Percentage transported to control benefit or deficit (−)
		One ocean	Two ocean	Three ocean	Total	Observed	Estimated[2]	
1969:								
Ice Harbor Dam (control)	25,313	43	3	0	46	0.182	0.792	—
John Day Dam (transported)	20,430	76	25	1	102	0.499	1.600	174
1970:								
Ice Harbor Dam (control)	18,347	12	58	1	71	0.387	0.729	—
John Day Dam (transported)	20,935	8	66	1	75	0.358	0.610	−7
Bonneville Dam (transported)	31,282	14	162	2	178	0.569	0.924	47

[1] Adjusted for initial tag loss

[2] Based on comparison of the known recovery of fish with magnetized wire tags at Little Goose Dam and the subsequent recovery of these and other marked fish at a hatchery upstream from Little Goose Dam. Returning fish identified at the dam were marked with dart and jaw tags and released to continue their migration upstream. Numbers of externally-tagged fish arriving at Dworshak Hatchery were compared with the recovery of other wire-tagged fish not previously detected and identified at Little Goose Dam.

turns from this release were 7% less than returns from controls).

Recovery of Marked Chinook Salmon in Commercial and Sport Fisheries

Although only 43 adult chinook salmon (Table 5) were recovered in the commercial and sport fisheries from juvenile releases in 1969, returns indicate a definite benefit from transportation. The benefit of transported fish (John Day-Bonneville releases combined) was 19%.

It was not possible to distinguish between returns of adults to the fishery from juvenile releases at Bonneville and John Day because of the loss of the identifying brands. Brands which would have enabled identification by release site were obliterated by gillnet abrasion. Transported and control groups of juveniles could be distinguished as adults by magnetic tags, but only two codes were used–one for the controls and one for the transported fish (Bonneville and John Day combined). However, if the percentage of adult returns obtained at Ice Harbor and Little Goose dams–where brands of fish returning from releases at Bonneville and John Day were visible–is applied to the total returns of adults as obtained in the commercial fishery, the benefit from transporting juveniles becomes 59% for chinook salmon transported to Bonneville Dam.

TABLE 5.–Comparison between transported and nontransported groups of chinook salmon based on numbers of transported and nontransported juvenile fish (released in 1969) that were captured as adults by commercial and sport fisheries in the lower Columbia River, February through August 1971 and 1972.

Location of fisheries	No. of salmon recaptured as adults	
	Transported	Nontransported
Upstream from Bonneville Dam (Indian fishery)	8	4
Downstream from Bonneville Dam	17	14
Total	25	18

Adult recoveries in the lower river commercial and sport fisheries from juvenile chinook salmon released in 1970 were insufficient (seven transported and eight control fish) for analysis of transport to control return ratios.

Returns of Adult Chinook Salmon to Spawning Grounds

Spawning ground surveys (Figure 2) and examination of tagged adult chinook salmon at Rapid River Hatchery near Riggins, Idaho, provided further information concerning benefits at their "home" destination from transport of juvenile spring- and summer-run chinook salmon.

In 1971, 12 tagged adult fish (from the 1969 juvenile release) were recovered from the Rapid River Hatchery; an additional 15 were from sport fishermen and spawning ground surveys. Of the total, 15 adults were from the transported groups and 12 from the control group. By adjusting from the ratio of John Day to Bonneville adult returns, we estimated that 12 of the 15 transported fish

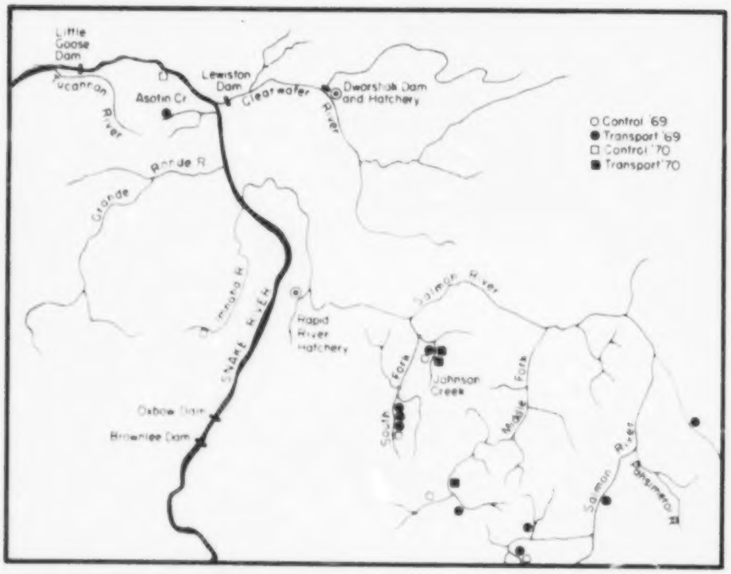
Little Goose Dam
Tucannon River
Asotin Cr
Lewiston Dam
Clearwater River
Dworshak Dam and Hatchery
○ Control '69
● Transport '69
□ Control '70
■ Transport '70
Grande Ronde R
Imnaha R
Snake River
Rapid River Hatchery
Salmon River
South Fork
Johnson Creek
Middle Fork
Oxbow Dam
Brownlee Dam
Salmon River
Pahsimeroi R

FIGURE 2.–Location of recoveries of tagged adult chinook salmon returning to spawning grounds from 1969-70 experiments.

were from the group released at Bonneville Dam. The transport benefit for the groups of juveniles released at Bonneville becomes 78% when computed on the basis of the number of juveniles released per group.

Too few tagged adult chinook (five Bonneville transports and one control) from the 1970 juvenile releases were collected in 1972 from all sources to make conclusions regarding the effect of transportation.

Discussion

Results from this study, which was a continuation of a study begun by Ebel et al. (1973), corroborated earlier findings, i.e., homing of adults after transportation downstream as juveniles was not seriously affected and survival was increased. Throughout this study, we found no evidence of straying among adults returning from the experimental releases. All comparisons between the adult returns from transported and control groups of juvenile chinook salmon and steelhead trout indicated that survival was definitely increased by transporting juvenile fish to a release site downstream from Bonneville Dam.

We have been particularly concerned with how the percentage return from these experiments might compare with that of unhandled or undisturbed juvenile migrants. Some insight into this matter is shown by a comparison between estimated adult returns from juveniles marked and released as controls and returns of unhandled adult fish to Rapid River Hatchery in Idaho (Table 2); the data indicate that survival of chinook salmon released in our 1968 experiment was greater than that indicated for salmon returning to the Rapid River Hatchery. Adult returns from controls released in 1969 were comparable to hatchery returns, but returns from those released in 1970 were lower than returns to the hatchery.

It is assumed that some stress was placed on juveniles in the collection, handling, marking, and transport processes. These cumulative stresses were not outwardly apparent in the physical condition of the juvenile smolts at the time of handling, but differences in survival of returning adults indicated that condition of the fish at the time of marking must have varied among years.

Our collection methods were changed in 1970 by addition of a fish pump; this added a pumping stress to our fish handling process. Although Park and Farr (1972) indicate no immediate mortality or observed stresses due to pumping from the facility, it is possible there could have been significant delayed effects. The effect of pumping on juvenile chinook salmon and steelhead trout—when added to other cumulative stresses associated with handling in our transport process—is indicated by the lower percentage of adult returns from control releases of juveniles in 1970.

Although smaller numbers of juvenile chinook were released in 1969-70 than in 1968 and a correspondingly small number of adults returned, we believe that the lower percentage of returning adults does indicate that stress factors due to handling were higher in 1970 than in 1969. The addition of two dams—Lower Monumental and Little Goose—placed in operation in 1969 and 1970, upstream from Ice Harbor Dam, must also be considered. Fish had to pass through Lower Monumental Reservoir and Dam in 1969 before being collected at Ice Harbor Dam. In 1970, they had to pass through both reservoirs and dams before being collected. Supersaturation of dissolved nitrogen also became a problem between Little Goose and Ice Harbor dams at this time. Turbines from both Lower Monumental and Little Goose dams were not scheduled for installation until after the spring freshet and as a result large volumes of water had to be passed over the spillways, causing dissolved gas concentrations to be high; a large percentage of the fish arriving at Ice Harbor Dam exhibited obvious signs of gas bubble disease.

If we use the percentage adult returns in relation to juveniles released at the Rapid River Hatchery in Idaho as an indicator of the rate of return of naturally migrating chinook salmon and we compare our percentage return figures, we find our estimate of return of controls was 4.3% in 1968—much higher than the 0.48% adult return recorded for Rapid River Hatchery[1]. The estimated control return of 0.497% for the 1969 outmigration is comparable to the 0.493% return to Rapid River Hatchery, but estimated returns from controls released in 1970 dropped to 0.323% whereas the return to the Rapid River Hatchery was 0.477%. Thus, the stresses placed on juvenile fish prior to collection, in addition to those involved in the handling process, conceivably were instrumental in causing the lower return of adults from the 1969-70 experiments.

When we examine adult returns from juvenile control releases of steelhead trout, we find that the percentage return from control releases of steelhead trout in 1969-70 were much greater than for comparable juvenile releases of chinook salmon. This indicates that the ability of steelhead trout to withstand the cumulative effects of stress is greater than that of chinook salmon.

Using the adult return percentage of steelhead trout to the Dworshak Hatchery from juvenile migrants released at that site in 1970 as a base indicator of the adult return of naturally migrating steelhead trout to Idaho streams, we find that our estimated adult returns from control releases to Ice Harbor and Little Goose dams of 0.792 and 0.729% (in 1969 and 1970, respectively) were somewhat greater than the 0.682%[2] return to Dworshak Hatchery. When our adult control returns are adjusted for the upriver sport catch on steelhead trout, our revised return (0.713% from the juvenile control releases in 1969) was comparable to the 0.682% return to Dworshak Hatchery. The return from the 1970 (control) release of 0.598% was, however, less than the hatchery return of 0.682%.

Based on the foregoing rationale, we believe that our control releases of juvenile chinook salmon and steelhead trout in 1969 returned as adults at rates comparable to those of natural migrating salmonids and that benefits on survival to adults indicated for our transported salmon and steelhead trout represent real increases.

Studies to further define stress problems associated with diversion, collection, and handling of naturally migrating juveniles are currently underway. To maximize the effectiveness of a collection and transportation system, stresses from all sources must be minimized.

Conclusion

The homing of adult fish, captured during their seaward migration as juveniles and transported downstream (from Ice Harbor Dam to Bonneville Dam), was not reduced by the transport operation. Although numbers of returning adults were small, comparisons of returns of transported fish versus control fish to Ice Harbor Dam, the spawning grounds, and hatcheries in Idaho indicated that they "homed" satisfactorily. No evidence of straying of transported fish was observed in our surveys.

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[1] Pers. commun. Evan Parrish, Hatchery Manager, Rapid River Hatchery, Riggins, Idaho.

[2] Pers. commun. Einer Wold, Hatchery Pathologist, Dworshak Hatchery, Ahsahka, Idaho.

Adult returns indicate a definite benefit is achieved from transporting juvenile chinook salmon and steelhead trout from a collector dam (Ice Harbor) to a release site below Bonneville Dam. Transport benefits were lower than reported from releases made in 1968, but a benefit of 27-47% was still indicated. No steelhead trout were released at Bonneville Dam in 1969, but a 47% benefit was realized from transportation of juveniles to that site in 1970.

Data from returning adults indicate that in general the John Day release site was a poor one. In 1969, however, returns from juvenile steelhead trout releases there were 174% greater than controls. The reduced transport benefit for our John Day release can probably be best explained by the fact that juveniles must still pass over The Dalles and Bonneville dams before entering the ocean. These further stresses probably nullify any initial transport benefit.

The rate of adult return from those juvenile fish transported in 1969 was better than the adult returns from those transported in 1970. Data suggest that stresses to juveniles encountered prior to collection at Ice Harbor and the changed handling procedures in 1970 were a factor.

Literature Cited

BENTLEY, W. W., AND H. L. RAYMOND.
1969. Passage of juvenile fish through orifices in gatewells of turbine intakes at McNary Dam. Trans. Am. Fish. Soc. 98:723-727.

DURKIN, J. T., W. J. EBEL, AND J. R. SMITH.
1969. A device to detect magnetized wire tags in migrating adult coho salmon. J. Fish. Res. Board Can. 26:3083-3088.

EBEL, W. J., D. L. PARK, AND R. C. JOHNSEN.
1973. Effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. Fish. Bull., U.S. 71:549-563.

JEFFERTS, K. B., P. K. BERGMAN, AND H. F. FISCUS.
1963. A coded wire identification system for macro-organisms. Nature (Lond.) 198:460-462.

MIGHELL, J. L.
1969. Rapid cold-branding of salmon and trout with liquid nitrogen. J. Fish. Res. Board Can. 26:2765-2769.

PARK, D. L., AND W. E. FARR.
1972. Collection of juvenile salmon and steelhead trout passing through orifices in gatewells of turbine intakes at Ice Harbor Dam. Trans. Am. Fish. Soc. 101:381-384.

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COMPARATIVE VULNERABILITY OF FRY OF PACIFIC SALMON AND STEELHEAD TROUT TO PREDATION BY TORRENT SCULPIN IN STREAM AQUARIA

Predation on fry of salmon and trout by sculpin, *Cottus* spp., is intense in certain situations (Hunter 1959; Sheridan and Meehan 1962; Patten 1962, 1971a, 1972) or of little consequence in others (Ricker 1941; Patten 1971a, 1972). Variation in intensity may be related to such important causes as the environment or to specific differences of the predators or prey.

In this paper I report the comparative ability of steelhead trout, *Salmo gairdneri*, and of five species of Pacific salmon, *Oncorhynchus* spp., to avoid predation by torrent sculpin, *C. rhotheus*, in a fixed environment–stream aquaria. The vulnerability of a species of salmon or steelhead trout, as determined from this study, is related to known information on the duration of residency and behavior of a species in streams. These results help in the assessment of natural causes of mortality that affect the productivity of salmon and steelhead trout. The study was conducted in stream aquaria adjacent to Cedar River near Ravensdale, Wash., in 1966.

Facilities and Procedures

The facilities consisted of two stream aquaria and eight holding aquaria that received water from the Cedar River (more fully described by Patten 1971b). Two stream aquaria used for tests of predation were 2.4 m long and 0.6 m wide and high; water depth ranged from 2 to 18 cm depending on bottom contour. The eight holding aquaria used in the study (to incubate the eggs and maintain the young fish before tests) were 34 cm wide by 41 cm long by 36 cm high; water depth was 18 cm.

Water from the Cedar River was taken at a low dam and supplied by gravity flow to the head box and then to the stream aquaria. Each aquarium had a continuous flow. The water was usually clear, and temperatures recorded at 0800 ranged from 5° to 10°C during the course of the study.

The experimental procedure exposed salmon or trout fry to predation by torrent sculpin under pseudo-natural but controlled conditions. Torrent sculpin were collected by electrofishing in Soos Creek, Wash.; the salmon and steelhead trout fry were reared from eggs to insure that they had no previous experience with predators.

Eggs from pink salmon, *O. gorbuscha*, chum salmon, *O. keta*, sockeye salmon, *O. nerka*, fall chinook salmon, *O. tshawytscha*, coho salmon, *O. kisutch*, and from steelhead trout of Puget Sound stocks were placed in holding aquaria and covered with coarse gravel.

The salmonid fry were subjected to predation tests as soon as the yolk sacs were absorbed. Since the time of emergence from the gravel by the fry of these six species varies, the tests extended from March to June, during which period water temperatures (Table 1) and day lengths differed. The salmon and trout fry were not fed but could be seen mouthing particles entering the holding aquaria. I assume growth of fry negligible and size differences to be fixed by the species and race used. Observations of viability and vigor of fry in the holding aquaria were made before, during, and after testing as a standard of comparison for test fish. Samples of the salmon and trout fry were measured in millimeters from snout to fork of tail (Table 1); their volumes were determined by displacement in a graduated tube. Sculpins were measured in millimeters from snout to end of tail (Table 1).

Twenty sculpins were placed in holding aquaria without food the first day of the experiment. On the second day 10 fry of one species were placed in each stream aquarium and on the third day, 10 sculpins were quietly introduced at the downstream end of each stream aquarium. On the fifth day the fry surviving after 48 h were counted; then both predators and prey were removed. These subjects were not used again. Two to seven replicate tests were made for each species of salmon or trout (Table 1).

Comparative Survival of Salmon and Trout Against Predation

The positions and activities of the salmon, trout, and sculpins in the stream aquaria are first described because these varied between species, affecting predator-prey interrelations. The following sections report on the viability and vigor of fry and on the survival rates of the species of salmon and trout.

The positions and activities of a species of salmon or trout during daylight tests varied. Fish in the stream aquaria maintained positions and apparently fed; chinook and coho salmon displayed intraspecific aggression, indicating accommodation to the enclosure. All species were observed in the deepest areas of the stream aquaria where they distributed themselves vertically 1 cm from the bottom to the water surface. Most of the steelhead trout fry and some pink and chum salmon fry hid under rocks, but this behavior was seldom exhibited by the other salmon species except for short periods when they were frightened.

Torrent sculpin typically spaced themselves through the deeper parts of the stream aquaria. They were distributed through its length with the greatest number at the upstream end. They were inactive and curled around large rocks or partially buried themselves in areas with soft bottoms. The concealment of the sculpins was so complete that I often had to search for as long as 20 min to remove all of them after an experiment.

After the sculpins were placed in the stream aquaria, the salmon and trout fry, on recovering from the disturbance, modified their vertical distribution. Salmon fry reacted to an active sculpin by moving away laterally and upward. In the presence of sculpins all salmon fry increased their distance from the bottom to about 5 cm. Steelhead trout fry, that usually hid under rocks when undisturbed, moved off the bottom and maintained positions near the water surface when sculpins were present. Behavior of the steelhead trout fry was apparently more disturbed by sculpins than was that of the salmon fry.

Sculpins rarely stalked the fry in bright daylight but waited immobile for them to come

TABLE 1.–Survival of salmon and trout fry subjected to predation in 1966 by torrent sculpin, *Cottus rhotheus*.

Species	Date of testing	Water temp[1] (°C)	Test (prey) fish: Number	Test (prey) fish: Length range (mm)	Mean length of predator (mm)	Number of tests	Number of survivors: Total	Number of survivors: Range/test	Percentage survival
Chinook salmon	3-25 to 4-15	6.2	60	38-42	92.0	6	31	1-8	51.7
Chum salmon	5-16 to 5-23	8.7	60	35-38	98.7	6	3	1-2	5.0
Coho salmon	3-25 to 4-15	6.2	70	36-39	91.7	7	53	6-8	75.7
Pink salmon	3- 2 to 3-11	6.2	60	35-37	92.5	6	1	0-1	1.7
Sockeye salmon	4-15 to 4-19	6.1	20	41-43	97.5	2	4	1-3	20.0
Steelhead trout	5- 4 to 5-13	8.9	60	29-31	91.4	6	14	0-7	23.3

[1] Average temperature (°C) at 0800 for 2 days of test.

near. Then they made short, quick lunges at the prey. Little predation occurred during the day and I never observed a sculpin catching a salmon.

Stocks of fry used for testing appeared normal, healthy, and vigorous. A reserve of fry of a species was maintained in holding aquaria during and after testing without mortality—in fact dead or inferior fry were never observed over 2 yr. Pretest salmonids held in stream aquaria often maintained positions in the faster moving water. Individuals that may have been inferior as indicated by use of slow water shallows, by swimming at the downstream end, or by impingement on the outlet screen were never observed.

Results showed variation between rates of predation on a prey species, size of prey species, and on temperature and length of daylight during testing. Predation by torrent sculpin was least on coho and chinook salmon, intermediate on sockeye salmon and steelhead trout, while practically complete on pink and chum salmon (Table 1). Chi-square analysis showed significant differences between all species except for 2 of the 10 combinations tested: sockeye salmon-steelhead trout and pink-chum salmon. The number of survivors per test varied considerably for the chinook salmon and steelhead trout. Steelhead trout were relatively deep bodied but shorter than salmon fry and among the salmon, chum and pink were thin bodied (Table 1 shows lengths; body volume determinations indicated chinook, coho, and sockeye salmon had as much as twice the displacement of the other species). Testing of chum salmon and of steelhead trout was a month or two later in the spring when temperatures were higher (Table 1) and duration of daylight was longer than for other species.

Innate Predator Avoidance of Species

Differences in rates of predation on the study species are not well explained by observed differences in behavior, size of prey, ambient conditions, or predator related effects but may be due to innate behavior after emergence of fry from the gravel. The only species with greatly divergent behavior in the stream aquaria was the steelhead trout. Remaining near the water surface during day effectively removes them from the influence of sculpin predators; however, they may settle to the substrate at night, a time when sculpins are more effective predators (Patten 1971b).

The larger prey species, those having the longest body lengths and being relatively deep bodied, were not always those with the higher survival. Chinook, coho, and sockeye salmon were the largest. Chinook and coho had the highest survival but the sockeye salmon, the largest prey, had survival similar to the steelhead trout, the smallest prey. Chum and pink salmon were slim and as long as coho and longer than steelhead trout, but their survival was lowest of the species studied. If size of prey or satiation of predators from greater food volumes influenced rates of predation, these factors were apparently less important than other effects on a species level.

Length of day or temperature had no apparent effect on rate of predation. Sculpins are most predaceous on salmon at times of marginal light intensity (Patten 1971b), which might suggest they are more serious predators at times of shorter day lengths. Trends between intensity of sculpin predation on fry and temperatures observed during this and other studies have never been observed.

The data show strong interspecific variations of the study species in vulnerability to predation by the torrent sculpin. I suspect a difference in innate behavior exists; some species are better able to evade predation. Furthermore, the early life history and behavior of the study species may be linked to their predator avoidance abilities. Chum, pink, and sockeye salmon quickly migrate from a stream environment to the sea or a lake where they form schools (Mason 1974, has observed chum salmon forming loose aggregations in estuaries). Schooling may aid these species in avoiding predation (Shelbourn 1966). Chinook and coho salmon and steelhead trout on the average form loose aggregations in streams during a period of growth before migrating to the sea. Forming loose aggregations would increase feeding opportunities in streams. Density of predators may be high in this situation (Patten 1971a) and survival is attained by a well-developed avoidance response for chinook and coho salmon.

Steelhead trout fry had a comparatively high mortality among stream resident species that may have been related in part to their behavior during tests, to their small size or an inferior predator avoidance response. Their survival, at least during the early fry stage, may be increased by unavailability through selection of a protective habitat. Hartman (1965) described the microhabitat of recently emerged steelhead trout and coho salmon in the Chilliwack River, British Columbia, as shallows at stream edges or in close proximity to physical objects. Recently emerged steelhead trout fry, observed adjacent to my study area in the Cedar River in 1965-66, were rarely found along sandy shore areas but were commonly seen among rocks at depths of 1 to 5 cm—when disturbed they hid under the rocks. The use of extreme shallows by steelhead trout fry may in part be an innate response to predators since this type of habitat in streams is relatively barren of other fish.

Literature Cited

HARTMAN, G. F.
  1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 22:1035-1081.

HUNTER, J. G.
  1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16:835-886.

MASON, J. C.
  1974. Behavioral ecology of chum salmon fry (*Oncorhynchus keta*) in a small estuary. J. Fish. Res. Board Can. 31:83-92.

PATTEN, B. G.
  1962. Cottid predation upon salmon fry in a Washington stream. Trans. Am. Fish. Soc. 91:427-429.
  1971a. Predation by sculpins on fall chinook salmon, *Oncorhynchus tshawytscha*, fry of hatchery origin. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 621, 14 p.
  1971b. Increased predation by the torrent sculpin, *Cottus rhotheus*, on coho salmon fry, *Oncorhynchus kisutch*, during moonlight nights. J. Fish. Res. Board Can. 28:1352-1354.
  1972. Predation, particularly by sculpins, on salmon fry in fresh waters of Washington. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Data Rep. 71, 21 p. on 1 microfiche.

RICKER, W. E.
  1941. The consumption of young sockeye salmon by predaceous fish. J. Fish. Res. Board Can. 5:293-313.

SHELBOURN, J. E.
  1966. Influence of temperature, salinity, and photoperiod on the aggregations of chum salmon fry (*Oncorhynchus keta*). J. Fish. Res. Board Can. 23:293-304.

SHERIDAN, W. L., AND W. R. MEEHAN.
  1962. Rehabilitation of Big Kitoi outlet stream, Afognak Island, Alaska. Alaska Dep. Fish Game, Div. Biol. Res. Inf. Leafl. 11, 13 p.

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HERITABLE RESISTANCE TO GAS BUBBLE DISEASE IN FALL CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*[1]

Construction of a series of dams on the Columbia River has resulted in air-supersaturation of the river during spring and early summer. Air-supersaturation is caused by the entrainment of air in water at depths as great as about 15 m in the plunge basins of the spillways below each dam. The level of air-supersaturation varies according to the amount of water-flow over the spillways (Ebel 1969). Supersaturation levels which are known to be fatal to salmonid fishes (Rucker and Hodgeboom 1953; Westgard 1964; Ebel 1969; and Blahm et al. 1975) are often sustained in the Columbia River from April through July, the period when many juvenile salmonids emigrate to the ocean.

Salmonids vary greatly in their tolerance for supersaturation (Ebel 1969). If a portion of this variability is related to additive genetic factors, an increase in the average tolerance of salmon populations to air-supersaturation can be expected as a result of selection. The purpose of this study was to estimate the influence of genetic factors on resistance to gas bubble disease for fall chinook salmon, *Oncorhynchus tshawytscha*. Specifically, the objectives were: 1) To determine the heritability of resistance to death from gas bubble disease for a stock of Columbia River fall chinook salmon, and 2) to determine the inherent level of resistance to gas bubble disease for several fall chinook salmon stocks.

Methods

Estimation of Heritability

Juvenile fall chinook salmon representing 80 families were reared at the Abernathy Salmon Cultural Development Center, near Longview, Wash. The families were produced by mating 20 males to 80 females, 4 females per male, in a nested breeding experiment. One hundred fish from each family were marked by cold-branding (Everest and Edmundson 1967) when they were 4 mo old and their weights averaged 2 g. Each group of 100 fish received a unique mark.

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[1] This work was carried out in cooperation with the U.S. Fish and Wildlife Service, Oregon Fish Commission, Oregon Wildlife Commission, and Oregon State University.

Thirty marked fish from each family were put into each of three tanks (1.8 m in diameter and 0.3 m deep) at the Abernathy Center. These groups of 30 fish will be referred to as tank-families. The remaining 10 fish from each family were put into a similar tank as a control. The test tanks were supplied with 18.9 liter/min of water which was air-supersaturated to 130 ± 1.5%.

Two variables, time to death for each fish after exposure to air-supersaturated water and the percentage survival for each family after 36 h of exposure, were examined.

Water to be air-supersaturated was directed into a pump to create a line pressure of 1.4 kg/cm^2. A controlled amount of air was injected into the line through an air stone inserted at a joint in the line. Aeration occurred under pressure in a 1.5-m vertical section of line. The test water then entered a pressurized tank where excess air was vented. Air-supersaturated water from the pressure tank was then jetted below the surface into the test tanks.

Stock Comparisons

Since differences between stocks of fish in their resistance to gas-bubble disease arise from both genetic and environmental factors, the fish used in the present experiments were reared in one location under controlled conditions to minimize differences related to environment. Differences in the groups of fish tested then were assumed to have a genetic basis.

Locations on or near the Columbia River that are discussed in this report are the following approximate distances (kilometers) upstream from the Pacific Ocean: Abernathy Salmon Cultural Development Center, 72; Kalama Hatchery, 105; Bonneville Dam, 234; Little White Salmon Hatchery, 265; Little Goose Dam, 635.

Experiment I.–In the fall of 1972, eggs were taken from mature fall chinook at Little Goose Dam on the Snake River, and at Trask River Salmon Hatchery. Smolts migrating downstream from Little Goose Dam must pass over seven dams and swim through water which may be air-supersaturated up to 130% (Beiningen and Ebel 1971). The Trask River enters the Pacific Ocean about 80 km south of the Columbia River and has never been known to contain lethal levels of air-supersaturated water. Eggs obtained at the Trask River Salmon Hatchery were taken from a large number of crosses, and eggs obtained at Little Goose Dam were from crosses between two males and two females.

Fertilized eggs from each source were transported to Oregon State University where they were incubated at 9.5°C. The fry were fed for 2 mo before being exposed to 127% air-supersaturated water. At the time of testing, the fish weighed between 1.3 and 1.5 g.

Air-supersaturated water was produced by aerating water under a hydrostatic head of 3 m in a vertical column of 15.2-cm pipe. A regulated amount of air was injected into the lower portion of the column through four air stones. Water drawn from the bottom of the column was 123% air-supersaturated. This water was then heated to 13.5°C to attain the test level of 127 ± 2% supersaturation.

Experiment II.–In 1973, fall chinook eggs were obtained from Abernathy Salmon Cultural Development Center, Little White Salmon Hatchery, and Kalama Hatchery–all on the Columbia River–and from the coastal Trask River Salmon Hatchery. Eggs from fish at Columbia River hatcheries were taken on 2 October, and those from fish at Trask River Hatchery on 28 November. All eggs were taken to Oregon State University for incubation, rearing, and testing.

Because of differences in ages, the experimental groups had to be tested at different times. We held the test fish in a constant environment at equal densities during the rearing period. The fingerlings were reared at 13.5°C in a 5.2 m × 0.3 m × 0.3 m Plexiglas[2] tank which was divided into 16 sections. The sections were divided into four blocks of four tanks each. Fifty fish from each of the four stocks were put into one section in each of the four blocks establishing a randomized block design. Fish were reared for 50 days, at the end of which time they weighed from 1.0 to 1.7 g. Seven days before testing, each group of fish was marked with a group-specific cold brand.

The fish were exposed to 127 ± 2% air-supersaturated water at 11°C in a 16.5-liter tank. Time to 50% mortality, proportion dead in 96 h, and proportion dead in 150 h were determined. An apparatus similar to that described above for tests at the Abernathy Center was used in this experiment. In all tests, we measured the total uncompensated hyperbaric dissolved gas pressure with a Weiss saturometer.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Estimation of Heritability

Initial mortalities occurred 3 h after the test fish were placed in 130% air-supersaturated water. All fish were dead after 132 h. The grand means of time to death (hours) in the three tanks were 22.62, 24.66, and 25.04. Two fish died in the control tank.

Because of counting errors at time of marking, individuals per tank-family ranged from 5 to 54. Few tank-families varied greatly from the expected number per family (28.4) as was indicated by the harmonic mean (26.8). Because of the unequal numbers of individuals per tank-family and the large number of observations, an unweighted means analysis of variance was used (Kempthorne 1957). First, the unweighted means of each family in each tank were subjected to an analysis of variance (Table 1). Second, all observations were used in a one-way analysis of variance to compute the within tank-families (error) sum of squares. Because the distribution of time to death for fish in each tank followed a poisson distribution, a square root transformation of time to death was applied before the analysis of variance was carried out. The square root transformation is the most appropriate for poisson data (Bartlett 1936).

Variance components were estimated as:

$$\sigma_M^2 = (MS_M - MS_F)/tf = 0.027$$

$$\sigma_F^2 = (MS_F - MS_{MFT})/t = 0.041$$

$$\sigma_{MFT}^2 = (MS_{MFT} - (1/\bar{n}_h)MS_W) = 0.024$$

$$\sigma_W^2 = MS_W = 2.800.$$

The additive genetic variance, V_A, was estimated as $4\sigma_M^2$, and the total phenotypic variance, V_P, as $\sigma_M^2 + \sigma_F^2 + \sigma_{MFT}^2 + \sigma_W^2$. Heritability, h^2, or V_A/V_P, was $4(0.027)/2.892 = 0.037$. The standard error was 0.022 (Dickerson 1959).

Survival for each tank-family after 36 h of exposure to the test conditions ranged from 53.8 to 0%. The angular transformation was applied to these data before the analysis of variance described above was performed. The theoretical binomial variance, 821, was then used as an estimate of error variance. Heritability of resistance to gas bubble disease estimated in this analysis was: $V_A/V_P = 30.68/840.87 = 0.036$.

Stock Comparisons

Resistance to gas bubble disease by offspring of fall chinook salmon from Little Goose Dam and Trask River Salmon Hatchery exposed to 127% supersaturation in Experiment I differed markedly. Time to 50% mortality, averaged from two replicates, was 73.5 h for Trask River fish and 154 h for fish from Little Goose Dam; the difference of 80.5 (SE = 3.39) was highly significant.

The difference in time to 50% mortality in Experiment II (Table 2) between Columbia River and Trask River stocks (22.25 h; SE = 6.37) was

TABLE 1.—Analysis of variance of the square root of time to death for juvenile fall chinook salmon exposed to air-supersaturated water.

Source of variation	Degrees of freedom	Mean squares	Expectation of mean square
Tanks (*T*)	$(t-1) = 2$		
Males (*M*)	$(m-1) = 19$	0.575	$\sigma_{MFT}^2 + \frac{1}{\bar{n}_h}\sigma_W^2 + t\sigma_F^2 + tf\sigma_M^2$
Females within males (*F*)	$m(f-1) = 60$	0.250	$\sigma_{MFT}^2 + \frac{1}{\bar{n}_h}\sigma_W^2 + t\sigma_F^2$
Male-females by tanks (*MFT*)	$(mf-1)(t-1) = 158$	0.128	$\sigma_{MFT}^2 + \frac{1}{\bar{n}_h}\sigma_W^2$
Error (*E*)[1]	$N_{...} - mft = 6{,}566$	2.800	σ_W^2

where: m = number of males
f = number of females per male
t = number of tanks (replicates)
$N_{...}$ = total number of individuals
$\bar{n}_h$ = harmonic mean number of individuals per tank family = 26.82

[1] Error mean square obtained in separate analysis (see Kempthorne 1957:488).

TABLE 2.–Hours to 50% mortality (ET_{50}), and percentages dead in 96 h (P96) and 150 h (P150) for juvenile chinook salmon exposed to air-supersaturated water in Experiment II. Each value represents an average of four replicates; ranges are shown in parentheses.

Stock	ET_{50}	P96	P150
Abernathy	92.5 (70-116)	53 (43-64)	68.5 (63-80)
Little White Salmon	86.5 (82-94)	61 (57-67)	77.0 (75-80)
Kalama	73.8 (64-79)	64 (60-70)	86.0 (73-95)
Trask	62.0 (48-75)	70 (64-82)	86.8 (75-96)

TABLE 3.–Analysis of variance in time to 50% mortality for Trask and Columbia River chinook salmon (Experiment II).

Source of variation	Degrees of freedom	Mean squares	F
Total	15		
Blocks	3	367.7	3.02
Between stocks	3	739.5	6.07*
Columbia vs. Trask	1	1,485.2	12.19**
Within Columbia	2	366.6	3.01
Error	9	121.8	

*, **, statistical significance at the 0.05 and 0.01 levels, respectively.

significant (Table 3). Variation between the three Columbia River stocks was not significant.

Similar comparisons were made from data summarized after 96 and 150 h of exposure (Table 2). On the average, differences between Columbia and Trask stocks remained significant, but variation between Columbia River stocks became significant only after 150 h of exposure (F = 5.01). This difference was between the Kalama stock and other lower Columbia River stocks, suggesting that a difference in resistance to gas bubble disease exists even between stocks separated by relatively short distances. The reason for the similarity of resistances between lower Columbia River stocks probably was their common origin: Abernathy brood stock were originally taken from Spring Creek and Willard hatcheries, both of which are located upstream from Bonneville Dam.

The much greater difference in time to 50% mortality between fish taken from Little Goose Dam and fish from the Trask River (80.5 ± 3.39 h) than between combined lower Columbia stocks and the Trask stock (22.25 ± 6.37 h) indicates that fall chinook salmon migrating as far as Little Goose Dam are more resistant to gas bubble disease than are lower Columbia River stocks. This conclusion could be made only by comparing results from Experiments I and II, and by assuming that the results were not biased by the small number of crosses made at Little Goose Dam.

Discussion

Differences between stocks indicated that selection for phenotypes with greatest resistances to gas bubble disease has occurred in the Columbia River. This conclusion was supported by the observation that stocks with the longest histories of exposure to air-supersaturated water were most resistant to gas bubble disease.

Because additive genetic variance contributing to the observed differences probably has been reduced, and reduced at an unknown rate, it is impossible to estimate accurately the selection intensities that must have occurred in the past to produce the differences in resistance observed between Trask and Columbia River stocks. The low heritability for resistance to gas bubble disease in fall chinook salmon indicates that no great increases in resistance can be expected even at relatively high selection intensities.

The results further indicate that stocks transferred from coastal streams to hatcheries within the Columbia River drainage may experience high levels of mortality from gas bubble disease. On the other hand, Columbia River stocks may provide a source of brood fish that are resistant to gas bubble disease for stocking in other waterways.

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Literature Cited

BARTLETT, M. S.
1936. The square root transformation in analysis of variance. J. R. Stat. Soc. (Suppl.) 3:68-78.

BEININGEN, K. T., AND W. J. EBEL.
1971. Dissolved nitrogen, dissolved oxygen, and related water temperatures in the Columbia and lower Snake Rivers, 1965-69. U.S. Natl. Mar. Fish. Serv. Data Rep. 56, 60 p.

BLAHM, T. H., R. J. MCCONNELL, AND G. R. SNYDER.
1975. Effect of gas supersaturated Columbia River water on the survival of juvenile chinook and coho salmon. NOAA Tech. Rep. NMFS SSRF-688, 22 p.

DICKERSON, G. E.
1959. Techniques for research in quantitative animal genetics. *In* Techniques and procedures in animal production research, p. 56-105. Am. Soc. Anim. Prod., Beltsville, Md.

Ebel, W. J.
1969. Supersaturation of nitrogen in the Columbia River and its effect on salmon and steelhead trout. U.S. Fish. Wildl. Serv., Fish. Bull. 68:1-11.

Everest, F. H., and H. E. Edmundson.
1967. Cold branding for field use in making juvenile salmonids. Prog. Fish-Cult. 29:175-176.

Kempthorne, O.
1957. An introduction to genetic statistics. Iowa State Univ. Press, Ames, 545 p.

Rucker, R. R., and K. Hodgeboom
1953. Observations on gas-bubble disease of fish. Prog. Fish-Cult. 15:24-26.

Westgard, R. L.
1964. Physical and biological aspects of gas-bubble disease in impounded adult chinook salmon at McNary spawning channel. Trans. Am. Fish. Soc. 93:306-309.

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